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Trophic Status and Rearing Capacity of Smaller Sockeye Nursery Lakes in the Skeena River System

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TROPHIC STATUS AND REARING CAPACITY OF SMALLER SOCKEYE NURSERY LAKES IN THE SKEENA RIVER SYSTEM

by

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ABSTRACT

Shortreed, K.S., J.M.B. Hume, K.F. Morton, and S.G. MacLellan. 1998. Trophic status and rearing capacity of smaller sockeye nursery lakes in the Skeena River system. Can. Tech. Rep. Fish. Aquat. Sci. 2240: 78p.

The Skeena River system has one large sockeye (*Oncorhynchus nerka*) nursery lake (Babine Lake) and approximately 26 smaller lakes. In this study, we investigated 10 of the larger non-Babine nursery lakes in the system. We examined lake physics, chemistry, several trophic levels important to juvenile sockeye, and juvenile sockeye numbers, biomass, and diet. Collected data enabled us to document the lakes' trophic status and the current state of their plankton and limnetic fish populations. The data also enabled us to estimate the numbers of juvenile sockeye the lakes could sustain when at rearing capacity. Primary productivity of the lakes varied widely (seasonal average photosynthetic rates ranged from 33-265 mg $C \cdot m^{-2} \cdot d^{-1}$), but all lakes were oligotrophic with the exception of Kitwanga Lake, which was mesotrophic. Biomass and composition of the lakes' zooplankton communities also varied widely. Seasonal average macrozooplankton (>250 µm in length) biomass ranged 2 orders of magnitude from 17-1,770 mg dry wt/m^2. Copepods were the dominant zooplankton in most lakes, although the large cladoceran *Daphnia longispina* was dominant in Kitwanga Lake, and small cladocerans (principally *Eubosmina longispina*) dominated Johanson and Sustut lakes. Factors limiting lake productivity ranged from glacial turbidity (Kitsumkalum Lake) to extremely low nutrient levels (e.g. Morice Lake). Limnetic fish densities were low (<500/ha) in most lakes but Sustut Lake had a higher density of 1,793/ha (almost all were age-0 juvenile sockeye) and Alastair Lake had a high density of >6,200/ha (stickleback (*Gasterosteus aculeatus*) made up two-thirds of this number). Size of age-0 fall sockeye fry ranged from 0.8 g in Morice Lake to 6.1 g in Lakelse Lake. Age-1 sockeye fry were captured only in Johanson and Morice lakes. Our data indicate that sockeye stocks in most of these lakes are recruitment-limited, and that current production of sockeye from these smaller Skeena lakes is <25% of the maximum potential production. We provide recommendations on the most suitable techniques for restoration and/or enhancement of the sockeye stocks in each of the lakes; these include increased fry recruitment, nutrient enrichment, and competitor control, either individually or in combination.

RÉSUMÉ

Shortreed, K. S., J. M. B. Hume, K. F. Morton, and S. G. MacLellan. 1998. Trophic status and rearing capacity of smaller sockeye nursery lakes in the Skeena River system. Can. Tech. Rep. Fish. Aquat. Sci. 2240: 78p.

Le réseau de la rivière Skeena comporte un grand lac d'alevinage du saumon rouge (*Oncorhynchus nerka*), le lac Babine, et environ 26 lacs de plus petite taille. Cette étude a porté sur 10 des plus grands des lacs à alevinage de ce réseau, à l'exclusion du lac Babine, dont nous avons étudié les caractéristiques physiques et chimiques, plusieurs niveaux trophiques importants pour les saumons rouges juvéniles, ainsi que leurs effectifs, leur biomasse et leur régime alimentaire. Les données recueillies nous ont permis de documenter l'état trophique de ces lacs, ainsi que l'état actuel de leurs populations de plancton et de poissons limnétiques. Ces données nous ont aussi permis d'évaluer le nombre des saumons rouges juvéniles que ces lacs pourraient supporter (à pleine capacité d'alevinage). La productivité primaire des lacs présentait de fortes variations (les taux de photosynthèse saisonniers moyens étaient compris entre 33 et 265 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$), mais tous les lacs étaient oligotrophes à l'exception du lac Kitwanga, qui était mésotrophe. De plus, la biomasse et la composition des communautés zooplanctoniques des lacs présentait aussi de fortes variations. Les valeurs saisonnières moyennes de la biomasse du macrozooplancton (de plus de 250 μm de longueur) occupaient une fourchette de deux ordres de grandeur, soit de 17 à 1 770 mg /m^2 (en poids sec). Dans la plupart des lacs, les copépodes étaient l'espèce dominante de zooplancton, mais dans le lac Kitwanga, c'était plutôt le gros cladocère *Daphnia longispina* et, dans les lacs Johanson et Sustut, des petits cladocères (surtout *Eubosmina longispina*). Les facteurs limitant la productivité des lacs allaient de la turbidité glaciaire (dans le lac Kitsumkalum) à des teneurs extrêmement faibles en substances nutritives (p. ex. dans le lac Morice). Les densités des poissons limnétiques étaient faibles (inférieures à 500 poissons/ha) dans la plupart des lacs, mais celle du lac Sustut était plus élevée, avec 1 793 poissons/ha (presque tous des saumons rouges juvéniles de moins d'un an), et celle du lac Alastair était forte, avec plus de 6 200 poissons/ha [dont les deux tiers étaient des épinoches à trois épines (*Gasterosteus aculeatus*)]. Les poids des alevins d'automne de saumon rouge d'âge 0 étaient compris entre 0,8 g dans le lac Morice et 6,1 g dans le lac Lakelse. On n'a capturé des alevins de saumon rouge d'âge 1 que dans les lacs Johanson et Morice. Nos données indiquent que les stocks de saumons rouges de la plupart de ces lacs sont limités par le recrutement et que la production actuelle de saumons rouges des petits lacs du réseau de la Skeena est inférieure à 25 % de la production maximale possible. Nous présentons des recommandations concernant les techniques les plus appropriées pour le rétablissement et/ou l'accroissement des stocks de saumons rouges dans chacun des lacs, notamment un accroissement du recrutement des alevins, un enrichissement en substances nutritives et une limitation des espèces en compétition, individuellement ou combinées.

INTRODUCTION

In British Columbia (B.C.), adult sockeye (*Oncorhynchus nerka*) returns to the Skeena River system are second only to returns to the Fraser River, which is the world's largest single river producer of this economically important species. From 1954 to 1984, total annual sockeye returns to the Skeena River ranged from 1 to 3 million (Sprout and Kadowaki 1987). From 1985 to 1996 annual returns were higher and averaged 3.8 million, with an average escapement of 1.4 million (Wood et al. 1997). Unlike the Fraser River system, which has over 15 large lakes which are important nursery areas for juvenile sockeye, the Skeena system has only one very large lake (Babine) and approximately 26 smaller ones. Historically, over 10% of Skeena sockeye production was attributed to non-Babine stocks. This has declined to 5-10% since construction of the Babine Lake spawning channels in the late 1960's (McKinnell and Rutherford 1994). The commercial fishery for Skeena sockeye is a mixed-stock fishery where harvest rates on each stock can be highly variable. This mixed-stock fishery can result in a substantial by-catch of important recreational and/or commercial species such as chinook (*O. tshawytscha*), coho (*O. kisutch*), and steelhead (*O. mykiss*). This has resulted in harvest rates that are probably excessive for other Skeena salmon stocks whose run timing overlaps with returns of the larger and more productive Babine sockeye stocks (Sprout and Kadowaki 1987). Conversely, attempts to protect less productive Skeena stocks have resulted in escapements in excess of spawning ground capacity to enhanced streams in Babine Lake.

The Skeena Watershed Committee was formed in 1993 to include representatives from user groups (commercial, native and sport fisheries) and from the federal and provincial governments. One of its objectives was to develop strategies to harvest optimum numbers of the large Babine stocks while reducing by-catch of less productive stocks and species. If these strategies are successful, then sockeye spawning escapements to some Skeena lakes (except the major Babine stocks) may be increased. Therefore, it was important to determine the current productivity and rearing capacity of these smaller Skeena sockeye nursery lakes. Once rearing capacity, spawning ground capacity, and current escapements are known, the amount of stock rebuilding necessary to maximize sockeye production from each lake can be calculated. With these data, managers can determine whether maximum production from each lake can be achieved strictly from increasing escapements, or whether some additional enhancement technique (e.g. spawning channels, outplants, lake fertilization) is required.

To predict rearing capacity and optimum escapements for the study lakes, we used a rearing capacity model (the PR model) which has been described in detail elsewhere (Hume et al. 1996; Shortreed et al. 1998). Data suitable for applying this model were already available from four Skeena lakes (Alastair, Bear, Swan, and Morice) (Stockner and Shortreed 1979). In 1994 and 1995 we collected comparable data from six additional lakes (Johanson, Kitsumkalum, Kitwanga, Lakelse, Morrison, and Sustut).

The main objectives of this report are to present:

1. status of juvenile sockeye stocks in the 10 largest non-Babine Skeena nursery lakes;
2. trophic status of the lakes
3. status of the lakes' plankton communities;
4. juvenile sockeye rearing capacity and factors limiting productivity;
5. recommended escapements to the lakes; and,
6. potential stock enhancement/restoration techniques.

This study was carried out in conjunction with a similar study on Babine Lake (Hume and MacLellan, unpubl. data; Shortreed and Morton, unpubl. data). The combined results of these two studies will enable us to document the quality and quantity of the major sockeye nursery areas in the Skeena River system and the current status of the juvenile sockeye populations in the system.

DESCRIPTION OF STUDY LAKES

The study lakes vary widely in morphometry, geography, and climate. Elevation varies from <150 m at Kitsumkalum and Lakelse lakes to >1300 m at Johanson and Sustut lakes in the upper portion of the drainage basin (Table 1, Fig. 1). Freshwater migration distance for both emigrating smolts and returning adults ranges from 92 km for Alastair Lake to 575 km for Johanson Lake. Climate throughout the region is continental, but the severity of the winters increases with elevation and distance from the ocean. Mean annual precipitation ranges from 150-250 cm at Kitsumkalum Lake to 40-50 cm at Morrison Lake (Farley 1979). The lakes are located in several different biogeoclimatic zones, including the coastal western hemlock zone at Kitsumkalum Lake, the sub-boreal spruce zone at Morrison Lake, and the subalpine Engelmann spruce-subalpine fir zone at Johanson and Sustut lakes (Farley 1979). The lakes are dimictic, with duration of winter ice cover increasing with elevation and distance from the ocean.

Surface area of the study lakes ranges from 1.4 km^2 (Johanson) to 96 km^2 (Morice). Of the 10 Skeena nursery lakes in this study, only Morice exceeds 20 km^2 in area (Table 1; Fig. 2-6). Total Skeena sockeye nursery area is 671 km^2, with Babine Lake making up 71% of the total and lakes in this study most of the remainder. Mean depth of the study lakes ranges from 5 m at Kitwanga Lake to 81 m at Kitsumkalum Lake (Table 1). Human activity on the lakes and their surrounding drainage basins varies considerably. Some lakes and drainage basins (Johanson and Sustut) are relatively untouched by human activity, while others have or have had extensive activities such as logging (Kitsumkalum, Lakelse, Kitwanga, Morrison) or residential/recreational development (Lakelse). In addition, Lakelse Lake is heavily used for recreational activities such as fishing and boating.

There are approximately 16 additional Skeena lakes which are, or could be, utilized by juvenile sockeye but were not included in this study. They are Aldrich, Asitka, Atna, Azuklotz, Club, Damshilgwit, Dennis, Johnston, Kluatantan, Kluayaz, McDonell, Motase, Sicintine, Stephens, Slamgeesh, and Spawning lakes. These are small lakes (total area <25 km^2) and comprise only 3-4% of the total Skeena nursery area.

ADULT SPAWNERS

Sockeye spawning escapements to the tributaries of the Skeena River have been monitored and recorded since 1950. McKinnell and Rutherford (1994) carried out a comprehensive review of methods of estimating non-Babine adult sockeye. They concluded: *"The systematic collection of abundance data of known quality for non-Babine Lake sockeye salmon in the Skeena River Watershed is for the most part, absent for all life history stages."*. Consequently, the accuracy and precision of sockeye escapement data to the smaller sockeye lakes is poor and variable, primarily because of the wide variety of methods used (Cousens et al. 1982; Williams and Brown 1994). Escapement estimates to most of the smaller Skeena lakes are made either by foot surveys using dead plus live counts or by aerial surveys. The accuracy of these methods is unknown (Sprout and Kadowaki 1987) and they tend to produce large (from 20% to more than 8-fold) underestimates of the actual population size (Brett 1952; Cousens et al. 1982; Tschaplinski and Hyatt 1991). Fence counts provide the most accurate estimates (Johnston et al. 1986), but fences have been used in only two instances in the study lakes - from 1962-1967 in Williams and Scully creeks (tributaries to Lakelse Lake, McKinnell and Rutherford 1994) and from 1992-1995 in the Sustut River (downstream of Johanson and Sustut lakes, C. Shirvell, pers. comm.). Additional uncertainty is introduced because spawner sex ratios were not usually determined in Skeena lakes and the proportion of female spawners (FS) which spawned successfully is unknown. Both of these can vary considerably (Schubert and Fanos 1997).

With this caveat, available data indicate that until the early 1970's, total annual sockeye escapement to the study lakes averaged 60,000 and comprised about 15% of the total Skeena sockeye escapement (Les Jantz, DFO, Prince Rupert, pers..comm.). Average escapements declined to approximately 30,000 during 1970-1985 but have increased to around 60,000 in recent years (Fig. 7, 8). However, because of increases in escapements to Babine Lake, escapements to the study lakes now make up only about 5% of total Skeena sockeye escapement. It should be noted that the Babine Lake escapement is estimated reliably at the Babine River counting fence in contrast to estimates on other Skeena lakes (excluding recent Johanson and Sustut escapements). Largest non-Babine escapements have usually been to Alastair and Lakelse lakes, followed by those to Morice and Morrison lakes. In these lakes, average annual escapements were in the range of 7,500 to 12,000, with peaks of over 25,000 in some years (Fig. 7, 8). In recent years, Morice Lake escapements have usually exceeded 20,000. Bear, Kitsumkalum, and Swan lakes had average escapements of 2,300-4,200 fish per year but in recent years escapements to Bear and Swan lakes have increased to 13,000-16,000 adults. Kitsumkalum escapements have not exceeded 5,500. Escapements to Johanson, Kitwanga, and Sustut lakes have averaged less than 800 fish per year and have never exceeded 3,000. Highest recorded escapements to Johanson and Sustut lakes have occurred since the establishment of a counting fence in 1992 (C. Shirvell, Dept. Fish. and Oceans, Nanaimo, B.C.). For the last 10 years there has been little apparent change in escapements to Alastair, Bear, Lakelse, and Morrison lakes. Kitwanga Lake was surveyed too infrequently to discern trends. Estimates indicate that the number of sockeye spawners to the additional 16 Skeena nursery lakes makes up <1% of the total Skeena escapement.

METHODS

SAMPLING FREQUENCY

In the current study we collected limnological data from Johanson, Kitwanga, Kitsumkalum, Lakelse, Morrison, and Sustut lakes. Limnological data on Alastair, Bear, Morice, and Swan lakes were collected in earlier studies (Stockner and Shortreed 1979; Costella et al. 1982). In this study, lakes were sampled either in 1994 or 1995. Data were collected once monthly from May-October (n=6) except that Johanson and Sustut lakes were sampled 4 times from June-October because of their shorter growing season. Juvenile sockeye data were collected from all 10 study lakes on hydroacoustic and trawl surveys conducted once in either late summer (August) or fall (September or October) from 1993-1995.

LIMNOLOGICAL DATA

Physical variables

Lake surface areas were determined by digitizing lake shorelines from 1:50,000 topographic maps using a computerized digitizing pad. Surface area and area of each depth contour were digitized from available bathymetric maps, which were usually drawn with less precision. The ratio of surface areas in the bathymetric map to the topographic map provided a correction factor for the depth contours. Lake volumes were calculated by multiplying the mean of consecutive contour areas by the depth interval and summing over all depth intervals.

Temperature and conductivity profiles from the surface to 100 m or the lake bottom were obtained at each station with an Applied Microsystems conductivity, temperature and depth meter (Model STD-12). Isotherms were plotted by the SAS procedure Gcontour (SAS Institute Inc., 1990) from a grid of interpolated and smoothed unscaled data computed by the SAS procedure G3grid using a bivariate method described by Akima (1978). Li-Cor data loggers (model LI-1000) equipped with quantum sensors (model LI-192S) were used to measure photosynthetic photon flux density (PPFD: 400-700 nm) from the surface to the compensation depth (1% of surface intensity) and vertical light extinction coefficients were calculated. Euphotic zone depth (EZD) was assumed to equal the compensation depth. A standard 22-cm white Secchi disk was used to measure water transparency.

Chemical variables

We used an opaque Van Dorn bottle sterilized with 95% ethanol to collect all water samples. Sampling took place between 0800 and 1200 h. At each station, water from 4-6 depths within the euphotic zone was collected and equal volumes mixed in 20-L Nalge Lowboy carboys to provide an integrated sample. Replicate analyses were carried out on each integrated sample.

At stations with sufficient depth, we also collected a hypolimnetic sample from 30 m. In addition, at one station on each lake we collected discrete water samples from 6-9 depths down the water column. These samples were collected in 1-L polyethylene bottles. Discrete water samples were analyzed for nitrate, total phosphorus, and chlorophyll. From the integrated samples we determined concentrations of silica, total dissolved solids, particulate carbon, particulate nitrogen, particulate phosphorus, phytoplankton, picoplankton, and bacteria. At stations where discrete samples were not collected, nitrate, total phosphorus, and chlorophyll concentrations were determined from the integrated sample.

Chemical analyses were carried out according to methods given in Stephens and Brandstaetter (1983) and Stainton et al. (1977). For total phosphorus determination, clean screw-capped test tubes were rinsed with sample, filled, capped, stored at 4°C, and later analyzed using a molybdenum blue method after persulfate digestion. Water samples for the remaining nutrient analyses and chlorophyll determinations were kept cool and dark and filtered within 2-4 h. Water for dissolved nutrient analyses was filtered through an ashed 47-mm diameter Micro Filtration Systems (MFS) borosilicate microfiber filter (equivalent to a Whatman GF/F filter). Each filter was placed in a 47-mm Swinnex filtering unit (Millipore Corp.), rinsed with distilled, deionized water (DDW), and then rinsed with approximately 50 mL of sample. An acid washed, DDW rinsed borosilicate glass bottle was rinsed and filled with 100 mL of filtered water, capped, stored at 4°C in the dark and later analyzed for nitrate (Stainton et al. 1977). An additional 100 mL of sample was filtered into a clean, rinsed polyethylene bottle, stored at 4°C in the dark, and later analyzed for soluble reactive silicon and total dissolved solids. For determination of particulate phosphorus concentration we filtered 1-L of water through an ashed 47-mm diameter MFS filter, placed the filter in a clean scintillation vial, and later analyzed it using the method of Stainton et al. (1977). For chlorophyll analysis we filtered 250-mL of water through a 47-mm diameter, 0.45-μm Millipore HA filter. Filters were folded in half, placed in aluminum foil dishes, and frozen. They were later analyzed using a Turner fluorometer (Model 112) after maceration in 90% acetone.

Water for alkalinity determinations was collected in glass bottles which were filled completely (one bottle from each sampling depth) and sealed. Within 4 hr of collection a Cole-Parmer Digi-Sense pH meter (Model 5986-10) and Ross combination electrode were used to determine the pH and total alkalinity (mg $CaCO_3$/L) of these samples according to the standard potentiometric method of APHA (1980). Dissolved inorganic carbon (DIC) concentrations were calculated indirectly from pH, temperature, total dissolved solids and bicarbonate alkalinity.

Biological variables

Water for bacterioplankton enumeration was collected in sterile scintillation vials and preserved with two drops of formaldehyde. Bacterioplankton were later counted using the DAPI method described by Robarts and Sephton (1981). Eight random fields were counted on each filter and the counts converted to numbers/mL. Occasional blanks were prepared to check for significant background bacteria counts in the staining solution and rinse water.

For nano- and microphytoplankton enumeration and identification opaque 125-mL polyethylene bottles were rinsed with sample, filled, and fixed with 1-mL of Lugol's iodine solution. For analysis, each sample was gently mixed and a subsample was settled overnight in a settling chamber of 7-, 12- or 27-mL capacity. Transects at 187.5X and 750X magnification were counted using a Wild M40 inverted microscope equipped with phase contrast optics. Cells were identified to genus or species and assigned to size classes. Phototrophic picoplankton (cyanobacteria and eukaryotic algae <2 μm in diameter) were enumerated using the method described by MacIsaac and Stockner (1985). Within several hours of sample collection, 15 mL of sample water was filtered through a 0.2-μm Nuclepore filter counter-stained with Irgalan black. Care was taken to minimize exposure of the sample to light during sampling and laboratory processing. Filters were placed in opaque petri dishes, air-dried and stored in the dark at room temperature until analyzed. During analysis, each filter was placed on a wet 40-μm mesh nylon screen in a filter holder, 1-2 mL of filtered DDW were added to the filter column, and the cells on the filter were rehydrated for 3-5 min. Water was drawn through at a vacuum pressure of 20-cm Hg, and the moist filter was placed on a glass slide with a drop of immersion oil (Cargille Type B) and a coverslip. The Zeiss epifluorescence microscope used for picoplankton enumeration was equipped with a 397-nm longwave-pass exciter filter and a 560-nm shortwave-pass exciter filter, a 580-nm beam-splitter mirror and a 590-nm longwave-pass barrier filter. Filters were examined at 1250X magnification under oil immersion, and 30 random fields were counted. Phototrophic picoplankton were placed in four categories based on morphological characteristics, fluorescence color, and size categories (Stockner and Shortreed 1991). Categories were unicellular (USYN) and colonial (CSYN) cells containing phycoerythrin (*Synechococcus*), unicellular cells (RCYN) containing phycocyanin, and REUK were cells 1-2 μm in diameter with a visible chloroplast.

Photosynthetic rates

We measured *in situ* photosynthetic rates (PR) at every sampling date and station. PR was determined at 6-8 depths from the surface to below the compensation depth or near the lake bottom, whichever was shallower. At each depth two light and one dark 125-mL glass bottles were filled, inoculated with approximately 137 kBq of a ^{14}C-bicarbonate stock solution, and incubated at the original sampling depth. Incubations lasted 1.5-2 h between 0900 and 1200 h. To determine activity of the stock solution, at each station we inoculated three scintillation vials containing 0.5 mL of Scintigest (Fisher Scientific) with the stock. After incubation, bottles were placed in light-proof boxes and transported to the field laboratory where filtration started <2 h after incubation stopped. We filtered the entire contents of each bottle through a 25-mL diameter MFS glass fiber filter at a vacuum not exceeding 20-cm Hg. Filters were placed in scintillation vials containing 0.5 mL of 0.5 N HCl and lids were left off the vials for 6-8 hr. All vials were stored cool and in the dark. Within a few days of the incubations, 10 mL of Scintiverse II (Fisher Scientific) was added to each scintillation vial and samples were counted in a Packard Tri-Carb 4530 liquid scintillation counter. Quench series composed of the same scintillation cocktail and filters used for samples were used to determine counting efficiency and Strickland's (1960) equation was used to calculate hourly PR. PR was converted from hourly to daily rates using light data collected with a Li-Cor Model LI-1000 datalogger and Li-Cor 190SA quantum sensors located near the lake being sampled. In lakes sampled prior to 1980 (Stockner and Shortreed

1979; Costella et al. 1982), scintillation cocktails in vials used for determining activity of the stock were not alkalized. Consequently, PR data we reported for those years overestimated actual PR by a factor of 1.49 (Kobayashi 1978). We divided PR data collected prior to 1980 by this factor to ensure compatibility with more recent data.

Zooplankton

Replicate zooplankton samples were collected at every station with a 160-µm mesh Wisconsin net (mouth area = 0.05 m^2) hauled vertically to the surface from 30 m or near bottom (if shallower). All samples were placed in 125-mL plastic bottles and preserved in a sucrose-buffered 4% formalin solution (Haney and Hall 1973). Zooplankton (except rotifers) were later counted, identified to genus or species using Balcer et al. (1984) and Pennak (1978), and measured with a computerized video measuring system (MacLellan et al. 1993). Measurement of body length was carried out as described by Koenings et al. (1987). Zooplankton biomass (milligram dry weight) was calculated with species-specific length-weight regressions adapted from Bird and Prairie (1985), Culver et al. (1985), Stemberger and Gilbert (1987), and Yan and Mackie (1987).

Calculation of seasonal averages and total annual carbon production

Seasonal averages for each lake were calculated as time-weighted means of data obtained during the growing season (defined as May 1-October 31). Seasonal average PR (PR_{mean}) was multiplied by the lake's surface area to give total seasonal PR (PR_{total}) in tonnes C/lake. In study lakes with mean depths <10 m (Kitwanga, Lakelse, and Sustut), PR_{total} was adjusted for bathymetry by computing seasonal average volumetric PR within specific depth intervals, multiplying it by the volume of the depth interval, and summing values for each interval. In deeper lakes (e.g. small littoral area), this adjustment was unnecessary, since it did not change PR_{total}. The contribution of littoral periphyton to total PR was not measured in this study, but given appropriate morphometry and water clarity, it can be more than half of total PR in the littoral zone (Loeb et al. 1983; Hawes and Smith 1994; Axler and Reuter 1996). The importance of the littoral zone to limnetic fish species is variable (France 1995) and the extent to which periphyton PR affects a lake's rearing capacity for juvenile sockeye is not known for our study lakes. To adjust PR model predictions for periphyton PR in the shallow study lakes, we assumed it was equal to phytoplankton PR in that proportion of the lake's surface area that was within the littoral zone. PR_{total} (adjusted for bathymetry) was increased by 90% in Kitwanga Lake, 45% in Lakelse Lake, and 95% in Sustut Lake. These estimates of PR_{total} were then used in the PR model to estimate optimum escapements and maximum smolt output from the study lakes (Shortreed et al. 1998).

JUVENILE SOCKEYE

Juvenile sockeye data were collected from the 10 lakes using hydroacoustic and trawl surveys carried out in late summer (August) or fall (September or October) from 1993-1995. All sampling was done during the hours of darkness when fish were dispersed near the thermocline and within the working range of the trawl and hydroacoustic system (McDonald and Hume 1984;

Burczynski and Johnson 1986; Levy 1990). Prior to hydroacoustic surveys, we divided the larger lakes (Kitsumkalum, Lakelse, and Morice) into 2 or 3 sections based on lake morphometry. Within each section, 2 to 3 evenly spaced hydroacoustic transects were established. Data from each transect were averaged to provide a mean estimate of density for each section. Mean density was multiplied by the surface area of the section to provide a population estimate for the section and then summed to provide a total population estimate for the lake. Mean lake density was calculated by dividing the lake population estimate by the total surface area. Variances were calculated for the density of each section and were then weighted by the square of the section area. The sum of the weighted variances was divided by the square of the lake area to provide a variance for the lake population estimate. Where a lake had only one section, simple variance was calculated for the density, which was then multiplied by the square of the lake surface area to provide a population variance. In this paper we report two times the standard error as an estimate of the confidence limits.

In Kitsumkalum, Lakelse, and Morice lakes we used a 7-m boat equipped with a 3x7 m closing midwater trawl (Enzenhofer and Hume 1989) and a Biosonics 105 dual beam echosounder. The echosounder used a 420 kHz dual beam (6°/15°) transducer. Data were digitally recorded for later echo integration and *in situ* target strength estimation (Burczynski and Johnson 1986) using a Biosonics Echo Signal Processor with a model 221 echo integrator and a model 228 dual beam processor. Target strengths and mean backscattering cross sections of fish were determined at each transect from data collected at 40 log R (R=distance to target) and target density was determined from echo integration of data collected at 20 log R. Target strength and equipment scaling factors were used to scale the echo integration to provide an estimate of fish density in each transect.

In Alastair, Bear, Johanson, Kitwanga, Morrison, Sustut, and Swan lakes we used two 4-m inflatable boats equipped with a 2x2 m midwater trawl (Hyatt et al. 1984; Gjernes 1979) and a Simrad EY-M single beam echosounder which used a 70 kHz 14° transducer. Data were collected at 40 log R and were recorded on dry chart paper for later analysis. Fish density at each depth interval and transect were determined by counting fish targets on the paper chart and dividing by the measured transect length and calculated beam width. This density was then multiplied by the surface area of the midpoint in the depth range to provide the number of fish at each depth range. These were summed over all depth ranges to provide a total transect population estimate and then divided by the area at the surface to provide the total density for each transect. This procedure was modified from Hyatt et al. (1984).

The magnitude of the difference between population estimates obtained from the two acoustic techniques used in this study is unknown, as is the accuracy of the two techniques. Parkinson et al. (1994) found that at densities from 250-1,500/ha, population estimates obtained using echo counting yielded densities 1.65x greater than those obtained using echo integration. Their echo counting method used a duration-in-beam technique to determine the effective beam width for the targets being counted, while our study used a nominal beam width. Duration-in-beam is an *in situ* method of determining beam width (Thorne 1988) and often yields an effective beam width larger than the nominal one. Consequently, it is possible that the echo counting technique used in this study provided estimates which were higher than the echo integration estimates by even more than the 1.65x reported by Parkinson et al. (1994). However, at densities <250/ha echo counting and echo integration yield similar results. At higher densities, individual targets are not discernible and echo counting becomes ineffective. The upper density limit for echo counting to provide reasonable data is dependent on vertical and horizontal distribution of limnetic fish, but can be as low as 3,000/ha.

Fish were collected from each lake with midwater trawls. Trawls were from 5-45 min in duration and were made at locations and depths suggested by fish targets on the echosounder. All captured fish were anaesthetized and killed upon capture with an overdose of 2-phenoxy-alcohol and preserved in 10% formalin. Fish were kept in formalin for at least one month before lengths and weights were recorded. These data were used to determine species and age composition of the limnetic fish community. Age composition of *O. nerka* was determined from scales and from length frequency analysis.

Stomach contents from up to 20 sockeye/trawl were analyzed. To minimize bias caused by different digestion rates of prey, only fish collected within 3 h after the onset of darkness were examined. Samples consisting of the contents of 10 pooled stomachs (2 samples/tow) were subsampled with a Folsom plankton splitter and enumerated with a computerized video measuring system (MacLellan et al. 1993). Relative volume of prey types in the stomachs and an index of stomach fullness expressed as a percentage by volume were estimated using a technique modified from Hellawell and Abel (1971).

RESULTS

PHYSICAL

Seasonal average surface temperatures ranged from a low of 11.7°C at Johanson Lake to a high of 16.8°C at Lakelse Lake (Table 2). Depending on the lake, highest seasonal surface temperatures occurred from June to September, and ranged from 15°C in Kitsumkalum Lake to 21°C in Morrison Lake (Fig. 9-11). Average thermocline depths ranged from 4.5 m in Sustut Lake to 25.5 m in Kitsumkalum Lake (Table 2). Thermal stratification in Kitwanga Lake lasted longer and was shallower and more stable than any other lake in the study (Fig. 10). Least stable stratification occurred in Kitsumkalum Lake (Fig. 9). After initial warming (May-July), thermocline depths in the smaller lakes in this study exhibited little seasonal variation.

The study lakes exhibited substantial variation in water clarity, ranging from clear (Johanson, Sustut) to humic (Morrison) to glacially turbid (Kitsumkalum). Seasonal average Secchi depth was lowest (0.9 m) in Kitsumkalum Lake and highest (10.2 m) in Johanson Lake, as was average euphotic zone depth (EZD) (range: 3.8-21.4 m) (Table 2). Extinction coefficients ranged from 0.19 in Johanson Lake to 1.10 in Kitsumkalum Lake (Table 2). The lakes exhibited little seasonal variation in water clarity.

CHEMICAL

Most lakes in this study were slightly alkaline, with seasonal average pH ranging from 7.00 in Morice Lake to 7.46 in Kitwanga Lake (Table 3). None of the lakes exhibited any distinct seasonal trends in pH. Seasonal average total dissolved solids (TDS) exhibited a 2.4-fold range from 28 in Kitsumkalum Lake to 68 in Kitwanga Lake. Seasonal average total alkalinity exhibited a somewhat greater range, from 13.0 mg $CaCO_3$/L in Morice Lake to 59.5 in Kitwanga Lake (Table 3). Dissolved silicate also did not exhibit much seasonal variation and seasonal averages ranged from 0.23 mg Si/L in Alastair Lake to 2.25 mg Si/L in Sustut Lake (Table 3).

Average total phosphorus (TP) concentrations were 2.0 µg/L in Morice Lake and ranged from 3.3-7.4 µg/L in the remaining lakes (Table 3). We disregarded TP data for Kitsumkalum Lake because the considerable degree of glacial turbidity resulted in erroneously high results (Koenings et al. 1987; MacIsaac, pers. comm.). TP data from Alastair, Bear, and Swan lakes (Stockner and Shortreed 1979) were also disregarded because TP methods used prior to 1980 yielded inaccurate results (E. MacIsaac, unpublished data). Distinct seasonal trends in TP were not apparent. TP values at spring overturn (TP_{spr}) were 2 µg/L in Johanson Lake and ranged from 5-11 µg/L in the remaining lakes (Fig. 12a).

Nitrate concentrations were quite variable, both among lakes and seasonally within lakes. Seasonal average concentrations of epilimnetic nitrate ranged from near or below our analytical detection limit of 1 µg N/L in Johanson, Kitwanga, and Sustut lakes to 35.5 µg N/L in Kitsumkalum Lake (Table 3). Spring nitrate concentrations in the current study lakes ranged from <5-90 µg N/L (Fig. 12). Epilimnetic nitrate was reduced to <1 µg N/L for all or part of the growing season in all lakes except Kitsumkalum (Fig. 12b). In all of the current study lakes, summer epilimnetic nitrate concentrations were lower than hypolimnetic concentrations (Fig. 13-15). The hypolimnia of Johanson, Kitwanga, Lakelse, and Sustut lakes had low nitrate concentrations for most or all of each growing season but in the remaining lakes, summer hypolimnetic nitrate concentrations were more than 10 times higher than those in the epilimnion.

Concentrations of particulate C (PC), particulate N (PN), and particulate P (PP) exhibited little seasonal variation in any study lake, although highest concentrations tended to occur in spring. Ranges in seasonal average particulate concentrations were 187-373 µg C/L, 22-41 µg N/L, and 2.0-4.1 µg P/L (Table 4). PP concentrations in Kitsumkalum Lake are not listed because of analytical problems caused by the glacial turbidity. PP was not measured in Morice Lake. PC was lowest in Morice Lake and highest in Sustut Lake, PN was lowest in Kitsumkalum Lake and highest in Kitwanga Lake, and PP was lowest in Johanson Lake and highest in Sustut Lake. Molar ratios of the particulate elements also varied considerably between lakes. C/N ranged from 5.5 in Morice Lake to 12.7 in Kitsumkalum Lake (Table 4). C/P was lowest (217) in Lakelse Lake and highest (340) in Johanson Lake. N/P ranged from 20 in Sustut Lake to 30 in Kitwanga Lake.

PHYTOPLANKTON AND BACTERIOPLANKTON

Seasonal average epilimnetic chlorophyll (CHL) concentrations were lowest (0.60 μg/L) in Kitsumkalum Lake and highest (2.74 μg/L) in Alastair Lake (Table 5). Seasonal maximum CHL occurred in May or June in all study lakes except in Kitsumkalum Lake, where highest CHL occurred in August (Fig. 16). Spatial and temporal trends in CHL were quite variable between the study lakes (Fig. 17-19). In Morrison Lake, highest CHL (2-3 μg/L) occurred in the euphotic zone from June to August. CHL was highest at the water surface in June in Lakelse Lake and in August in Kitsumkalum Lake. Johanson Lake had a hypolimnetic CHL maximum of 1.5-2 μg/L at approximately 20 m, which corresponded to the bottom of the euphotic zone. In Kitwanga and Sustut lakes the euphotic zone extended to or near the lake bottom, and both lakes had summer CHL maxima (highest values were 3.0-3.5 μg/L in Sustut Lake and 4.0-4.5 μg/L in Kitwanga Lake) near the sediment-water interface (Fig. 18,19).

Photosynthetic rates (PR) were highly variable among lakes. PR_{mean} varied 8-fold, from 33 mg $C \cdot m^{-2} \cdot d^{-1}$ in Kitsumkalum Lake to 265 mg $C \cdot m^{-2} \cdot d^{-1}$ in Kitwanga Lake (Table 5). Distinct seasonal trends were not evident, with timing of the seasonal maxima ranging from spring to fall in the study lakes (Fig. 16). Depth profiles of PR also exhibited considerable variation between lakes. Kitsumkalum and Morrison lakes exhibited the shallow PR maxima indicative of rapid light attenuation (Fig. 20). In Lakelse Lake, maximum PR occurred below the surface at approximately one-half the EZD, while both Kitwanga and Sustut lakes had distinct PR maxima near the bottom of the EZD. In Johanson Lake, PR remained low and relatively constant for much of the EZD, a profile which is typical of clear, highly oligotrophic lakes (Fig. 20).

Seasonal average epilimnetic autotrophic picoplankton (APP) numbers ranged from 1.19×10^4/mL in Kitsumkalum Lake to 5.08×10^4/mL in Morrison Lake (Table 5). In most lakes, lowest APP numbers occurred in spring and highest abundance occurred in summer or early fall (Fig. 21-23). In Johanson, Kitsumkalum, and Sustut lakes, USYN (unicellular *Synechococcus*) made up >95% of total APP numbers (Fig. 21,23). In Kitwanga and Lakelse lakes, USYN made up 66 and 76% of total picoplankton (respectively), but in Morrison Lake USYN made up only 2% of total picoplankton. After USYN, CSYN (colonial *Synechococcus*) was the most numerous picoplankton. Although CSYN was not present in Johanson and Kitsumkalum lakes, it made up from 3% of total numbers in Sustut Lake to 56% in Morrison Lake. RCYN (unicellular picoplankton containing phycocyanin) were abundant (40% of the total) only in Morrison Lake.

Highest seasonal average nano-phytoplankton (NPH) numbers (1.53×10^3/mL) were found in Morrison Lake and the lowest numbers (0.26×10^3/mL) occurred in Johanson Lake (Table 5). Glacial particles in Kitsumkalum Lake interfered with enumeration of NPH, so no NPH data are presented for this lake. Seasonal NPH maxima occurred in spring in Kitwanga and Lakelse lakes, and in fall in Morrison Lake (Fig. 24). In the remainder of the lakes, NPH did not exhibit distinct seasonal variability. Average micro-phytoplankton numbers (MPH) were 3.97×10^3/mL in Sustut Lake and were much lower in the remainder of the lakes, ranging from 130/mL-1.11×10^3/mL (Fig. 24, Table 5).

Bacterioplankton numbers did not exhibit distinct seasonal trends except that highest numbers tended to occur in August or September. Highest seasonal average bacteria numbers of 1.92×10^6/mL occurred in Kitwanga Lake and the lowest concentration (0.64×10^6/mL) occurred in Johanson Lake (Table 5).

ZOOPLANKTON

Zooplankton community structure and biomass exhibited considerable variation among lakes. Seasonal average macrozooplankton biomass ranged 2 orders of magnitude from 17 mg dry wt/m^2 in Johanson and Sustut lakes to 1,770 mg dry wt/m^2 in Kitwanga Lake (Table 5). Macrozooplankton biomass (dry weight) was highest (3,000 mg/m^2) in June in Kitwanga Lake, declined to 1,500 mg/m^2 by July, and slowly declined further to 1,000 mg/m^2 by October (Fig. 25). In Kitsumkalum Lake, macrozooplankton biomass was highest (190 mg/m^2) during August and September. It was highest (approximately 1,000 mg/m^2) in June and July in Lakelse and Morrison lakes and was low (<40 mg/m^2) throughout the season in Johanson and Sustut lakes (Fig. 25).

Dominant zooplankton also varied among lakes. Biomass of *Daphnia* spp. (principally *Daphnia longispina*) was also highly variable, ranging from 63% of total biomass in Kitwanga Lake to <1% in Kitsumkalum Lake (Table 5,6). In Kitwanga Lake, *Daphnia* biomass increased from 200 mg/m^2 in May to 2,000 mg dry wt/m^2 in late June, decreased to 800 mg/m^2 by late July, and ranged from 800-1,200 mg/m^2 for the remainder of the growing season (Fig. 26). *Daphnia* biomass in the other study lakes was much lower, with slight increases in biomass in July in Lakelse, Morrison, and Sustut lakes, and in October in Johanson and Sustut lakes. Bosminidae (primarily *Bosmina longirostris*) were present in all study lakes but were dominant only in Johanson and Sustut lakes, where they made up 70% of total biomass (Table 5, 6). In Kitsumkalum, Kitwanga, Morrison and Sustut lakes, bosminid densities were low and exhibited little seasonal variation (Fig. 27). In Lakelse Lake, bosminid biomass increased from 20 mg/m^2 in June to 190 mg/m^2 in July, then quickly declined to <20 mg/m^2 for the remainder of the growing season. Johanson Lake bosminids increased slowly from June to October to a seasonal maximum of 30 mg/m^2 (Fig. 27).

Cyclopidae (mainly *Cyclops scutifer* and to a lesser extent *Diacyclops thomasi*) were present in all study lakes, making up 8-28% of total biomass except in Lakelse Lake, where cyclopoid biomass (as dry weight) made up two-thirds of the total (Table 5,6). In Kitwanga Lake, cyclopoid biomass declined from a high of 1,100 mg/m^2 in May to 100 mg/m^2 in September, while both Kitsumkalum and Lakelse lakes had mid-August peaks (Fig. 28). Cyclopoid biomass in Morrison Lake ranged from 100-300 mg/m^2 and in Johanson and Sustut lakes from 1-9 mg/m^2, with no seasonal trends apparent. Diaptomid (*Leptodiaptomus ashlandi* and *L. pribilofensis*) biomass exhibited considerable variation, comprising <1% of total biomass in Johanson and Sustut lakes and 85% of the total in Kitsumkalum Lake (Table 5, 6). In Morrison and Kitwanga lakes, diaptomid biomass increased to its highest level in June then declined through the growing season to <100 mg/m^2 in October (Fig. 29). In contrast, diaptomid biomass in Kitsumkalum Lake was highest during the latter portion of the growing season (August-October). Diaptomid biomass in Sustut, Johanson and Lakelse lakes was low, without obvious seasonal trends (Fig. 29). The calanoid copepod *Epischura nevadensis* made up 9% of total macrozooplankton biomass in Lakelse Lake and <2% of macrozooplankton biomass in the remainder of the lakes. It was not found in Johanson and Sustut lakes. Another large calanoid copepod, *Heterocope septentrionalis*, occurred only in Morrison Lake, where it made up 14% of total biomass (Table 6). It had a bimodal seasonal distribution with peaks in June and October.

Large pelagic invertebrates occasionally caught but not quantitatively sampled by the methods used in this study were *Leptodora kindtii* in Kitwanga and Morrison lakes, chironomid larvae in Kitsumkalum, Kitwanga, and Sustut lakes, and *Neomysis mercedis* in Lakelse Lake.

LIMNETIC FISH

Sockeye

Mean size of fall age-0 sockeye fry ranged from 0.8 g in Morice Lake to 6.1 g in Lakelse Lake (Table 7). Fall fry data were not collected from Johanson or Sustut lakes, but in late August average weight of fry in both Johanson and Sustut lakes was about 1.0 g. Fall fry from Morrison and Bear lakes were relatively large (4.3 g and 3.9 g, respectively), while fry from Alastair, Kitsumkalum, and Swan lakes all averaged <2 g (Table 7).

Age-0 sockeye fry densities exhibited considerable variation, ranging from 77/ha in Kitwanga Lake to 1,994/ha in Alastair Lake (Table 8). Lakelse Lake was the only lake where the limnetic population was estimated using echo integration and the density estimate (400 fish/ha) was between 250 and 1500 fish/ha. Scaling this data by the conversion factor of 1.65 found by Parkinson et al. (1994) would elevate the estimate to approximately 500 age-0 sockeye/ha and 150 stickleback/ha. Because of high limnetic fish densities in Alastair Lake, echo counting was an inappropriate acoustical technique. Therefore, the estimated total limnetic fish density of 6,165/ha is a minimum estimate only. Juvenile sockeye densities were <200/ha in 4 of the 10 study lakes and were <500/ha in all lakes except Alastair (1,994/ha) and Sustut (1,779/ha) (Table 8).

Juvenile sockeye distribution within the lakes was heterogeneous, with a four-fold variation in age-0 sockeye density between transects in Alastair and Morrison lakes and a 50-fold variation in Kitsumkalum and Lakelse lakes. Lakes with mean depths <20 m (Bear, Johanson, Kitwanga, Lakelse, and Sustut) had highest densities in the deepest lake areas. Highest densities in Kitsumkalum Lake were in the deeper northern end of the lake and in Morice Lake they were found in the south-central portion of the lake. Swan Lake had highest densities in the main basin of the lake with lower densities among the lake's numerous islands. Juvenile sockeye distribution within a lake is highly dynamic, so these data do not necessarily indicate the only important lake rearing areas.

We captured age-1 sockeye in Johanson and Morice lakes only. In Morice Lake, abundance of age-1 sockeye was estimated from dual beam target strength information because of the small sample size in the trawl catch. The target strength data indicated some spatial mixing of the two age classes, but the larger fish appeared to occupy a slightly deeper layer than the age-0 sockeye. Age-1 densities in Johanson Lake were based on the trawl catch alone, as no target strength data were available. Age-1 sockeye in Johanson Lake were captured at a greater depth than age-0 sockeye. Estimates of age-1 sockeye densities were 18/ha in Morice Lake and 36/ha in Johanson Lake (Table 8). Mean weight of age-1 sockeye was 2.4 g (n=20) in Johanson Lake and 6.0 g (n=2) in Morice Lake (Table 7).

Other species

Other species of limnetic fish were found in all lakes except Johanson and Morice. Density and biomass of non-sockeye was highest in Alastair Lake, where stickleback (*Gasterosteus aculeatus*) density was >4,200/ha and comprised two-thirds of total limnetic fish numbers (Table 8). Density of limnetic fish other than sockeye was <200/ha in all other study lakes. In Kitsumkalum Lake, only one fish, a juvenile river lamprey (*Lamptera ayresi*), was captured in our trawls. A single whitefish (*Coregonus* sp.) was the only non-sockeye species caught in Sustut Lake and in Kitwanga Lake, a long-nosed sucker (*Catostomus catostomus*) was the only trawl-caught non-sockeye. In Bear Lake we found substantial numbers (180/ha) of juvenile whitefish in the limnetic zone. Morrison Lake had a diverse limnetic fish community, with redside shiners (*Richardsonius balteatus*), sculpins (*Cottus sp.*), and whitefish totaling 147/ha (Table 8).

Biomass

Age-0 sockeye biomass ranged from 0.06 kg/ha in Morice Lake to 3.39 kg/ha in Alastair Lake. Age-1 sockeye contributed 24% and 65% of the total sockeye biomass to Johanson and Morice lakes, respectively. Total limnetic fish biomass ranged from 0.17 kg/ha in Morice Lake to 8.35 kg/ha in Alastair Lake (Table 8). Juvenile sockeye biomass comprised the majority of limnetic fish biomass in most lakes, but in Alastair Lake, sockeye made up only 41% of total biomass (Table 8). Bear Lake had substantial numbers of limnetic whitefish, but unfortunately, they were not sampled.

Diet

Sockeye stomach fullness ranged from <20% in Morice Lake to 100% in Lakelse Lake (Fig. 30). Stomach contents also varied considerably among the study lakes. In the 3 lakes (Kitwanga, Lakelse, and Swan) where stomach fullness exceeded 75%, *Daphnia* made up over 80% of the volume of the stomach contents (Fig. 30). Alastair, Morice, and Sustut sockeye all had stomachs <30% full and bosminids made up the majority of their diet. Stomachs from Alastair Lake sticklebacks contained equal volumes of bosminids and unidentified immature insects. Unidentified immature insects were also an important component of the diet of Johanson Lake sockeye. In Kitsumkalum and Morrison lakes, calanoid copepods (mainly *Leptodiaptomous* and *Epischura*) comprised the majority of sockeye diet. Another calanoid copepod, *Heterocope*, was the principle prey item of Bear Lake sockeye (Fig. 30).

DISCUSSION

PHYSICS

Optimum escapements and juvenile sockeye rearing capacity of a lake are positively correlated to its trophic status and productivity (Hume et al. 1996; Shortreed et al. 1998). In turn, a lake's trophic status and productivity are affected by a number of abiotic factors, including thermal structure, light transmission, and water chemistry. Lake thermal structure also has a direct effect on the behaviour of juvenile sockeye, particularly on the magnitude of their diel migrations (Levy 1990). If epilimnetic temperatures exceed those preferred by sockeye, duration of their foraging in the epilimnion (where zooplankton densities are higher) may be reduced, reducing the grazing pressure on the zooplankton community and causing reduced sockeye growth rates (Levy et al. 1991; Hume et al. 1996). If a lake has a very weak or deep thermocline, if euphotic zone depths are very shallow, or if euphotic zone depths are substantially less than thermocline depths, then productivity may be controlled primarily by light availability.

Lakes in this study exhibited a wide range of temperatures, thermal regimes, and euphotic zone depths (Table 2). None of the lakes had summer temperatures high enough to increase sockeye mortality rates (Fagerlund et al. 1995), but for some portion of the growing season epilimnetic temperatures in most study lakes were high enough (Levy et al. 1991) to reduce sockeye foraging in the epilimnion (Fig. 9-11). McConnell and Brett (1946) carried out a limnological study of Kitwanga Lake 50 years before our study and recorded maximum summer surface temperatures of 18°C, which was similar to the maximum of 18.6°C recorded in our study.

Because they were shallow, Kitwanga and Sustut lakes had very small hypolimnia which were too small to provide a daytime refuge for juvenile sockeye. Of the 10 lakes in this study, euphotic zone depths were one-third to one-half deeper than thermocline depths in Johanson, Kitwanga, and Sustut lakes. Of these, Kitwanga and Sustut lakes were shallow and had euphotic zones extending to, or near to, the lake bottom, with the result that all, or almost all, of the water column was within the euphotic zone. Lakelse and Morrison lakes exhibited stable thermal stratification and had thermocline depths 50-75% deeper than euphotic zone depths (Table 2). In other B.C. sockeye nursery lakes, lakes with thermocline depths up to 40% deeper than the euphotic zone often provide effective rearing environments. Kitsumkalum Lake had a thermocline 7x deeper than the euphotic zone as well as a weakly stratified epilimnion (Table 2, Fig. 9), clearly indicating that production was limited by light availability.

The majority of B.C. sockeye nursery lakes are deep (i.e. large hypolimnia) and oligotrophic, conditions where depletion of hypolimnetic oxygen is unlikely to occur. However, Kitwanga Lake was shallow, strongly stratified (where it was deep enough), and productive. We did not measure oxygen concentration in this study, but in an earlier study of Kitwanga Lake, McConnell and Brett (1946) found that where a hypolimnion existed, summer oxygen depletion occurred. The depletion was restricted to a relatively small portion of the lake and so was unlikely to be a direct cause of increased mortality. However, for the duration of the depletion it would eliminate the hypolimnion as a coldwater refuge.

TROPHIC STATUS

Nutrient availability (primarily phosphorus) is often the most important factor controlling the trophic status of North American lakes (Dillon and Rigler 1974; Stockner and Shortreed 1985; Shortreed and Stockner 1986). For this reason, total phosphorus (TP) concentration (either seasonal average or spring overturn) has been a widely used variable in indices of trophic status (Vollenweider 1976). However, TP is a relatively insensitive indicator of a lake's productivity and for a variety of reasons may inaccurately characterize a lake's trophic status, particularly when the range in TP concentrations found in a suite of lakes is not large. In glacially turbid lakes (common in parts of western Canada and Alaska), analytical difficulties which result in substantial overestimates of total or biologically available phosphorus (Koenings et al. 1987; E. MacIsaac pers. comm.) make TP a poor indicator of productivity. Further, in turbid lakes (glacial or otherwise) light may be a more important limiting factor than nutrients (Koenings and Burkett 1987). In other lakes, the nitrogen supply may also be depleted for a portion of each growing season. In these lakes, co-limitation of nitrogen and phosphorus may occur (Suttle and Harrison 1988; Stockner and Shortreed 1994).

Based solely on TP, all lakes in this study were oligotrophic with the exception of Kitsumkalum Lake, which was mesotrophic (Vollenweider 1976). However, the glacial turbidity in Kitsumkalum Lake resulted in erroneously high TP values and other variables (to be discussed later) indicated that Kitsumkalum was actually the least productive lake in the study. Excluding Kitsumkalum Lake, the study lakes had a relatively minor 2.2-fold range (3.3-7.4 μg/L) in TP, with Johanson Lake having the lowest and Kitwanga Lake having the highest. Epilimnetic nitrate was depleted (<1 μg/L) for part or all of the growing season in all study lakes except Kitsumkalum, indicating some degree of nutrient co-limitation. Where this occurred, TP concentration tended to over-estimate the lakes' trophic status.

Chlorophyll (CHL) concentration has also been widely used as an indicator of trophic status. Further, the correlation of TP with CHL has been used to validate the use of TP as an indicator of trophic status. Forsberg and Ryding (1980) developed a trophic scale based on average chlorophyll concentration where CHL is <3 μg/L in oligotrophic lakes, 3-7 μg/L in mesotrophic lakes, and 7-40 μg/L in eutrophic lakes. Our study lakes had a 4.2-fold variation in CHL and based on this scale, all were oligotrophic. Kitsumkalum Lake had the lowest CHL and Alastair Lake, with an average CHL of 2.74 μg/L, had the highest. A third trophic state index using bacteria numbers and their correlation with CHL was developed by Bird and Kalff (1984). Based on this classification, our study lakes were oligotrophic ($<1.7 \times 10^6$ bacteria/mL) with the exception of Kitwanga Lake, which was mesotrophic (Table 5).

These indices use variables which are indicators of standing stock or biomass (TP, CHL, bacteria), while a lake's trophic status is set by its production rate. While standing stock is often correlated to production rate, many abiotic and biotic factors can affect and/or weaken the correlation. While rate measurements are generally more difficult to obtain than measurements of standing stock, they provide a direct estimate of a lake's productivity. In all study lakes we obtained a direct estimate of carbon production by measuring photosynthetic rate (PR), and so could correlate it to the various trophic state indices. Seasonal average PR varied 8-fold in the study lakes, with Kitwanga Lake the most productive and Kitsumkalum Lake the least productive (Table 5). Although TP, CHL, and bacteria tended to be positively correlated with PR, correlations were weak (Fig. 31). For reasons already discussed, Kitsumkalum Lake was a major outlier in the PR-TP correlation. PR and bacteria were significantly correlated only because PR and bacteria numbers in Kitwanga Lake were substantially higher than in any other study lake. PR and CHL were strongly correlated only if one outlier (Kitwanga Lake) was eliminated (Fig. 31). Why Kitwanga Lake is an outlier in this relationship cannot be conclusively demonstrated, but Kitwanga Lake had low planktivore densities and *Daphnia* biomass was >16x higher than in any other study lake (Table 6). *Daphnia* is both an effective grazer and nutrient recycler (Mazumder 1994a,1994b) and we suggest its high density in Kitwanga affected the relationship between biomass and productivity.

NUTRIENT LIMITATION

Ratios of sestonic and planktonic C, N, and P (C:P, C:N, N:P) have long been used to estimate the relative magnitude of nutrient limitation (Redfield et al. 1963; Healey and Hendzel 1980). In our study we did not determine elemental concentrations in the zooplankton community, but we did measure sestonic C, N, and P concentrations. C:N:P ratios ranged from 219:19:1 to 337:28:1, much higher than the average of 103:16:1 reported by Redfield et al. (1963) for marine phytoplankton. More recently, Elser and Hassett (1994) reported an average N:P ratio of 18 for marine seston. Elser and Hassett (1994) also reported an average seston N:P of 38 for a suite of lakes in central north America - higher than our observed N:P range of 20-30 (Table 4). With respect to other British Columbia lakes, C:N:P ratios in our study lakes were higher than most lakes in the Fraser River system, which had an average C:N:P ratio of 174:17:1 (K. Shortreed, unpubl. data). However, the ratio in our lakes was far lower than in coastal British Columbia lakes, where Stockner and Shortreed (1985) reported an average ratio of 473:47:1. C:N:P ratios in the study lakes are indicative of P-limited systems, with the degree of P limitation greater than in sockeye nursery lakes in the Fraser River system but less than in coastal British Columbia lakes.

This relative degree of nutrient limitation agreed well with direct measurement of lake productivity (PR). The 8-fold variation (33-265 mg $C \cdot m^{-2} \cdot d^{-1}$) in PR_{mean} in our study lakes was similar to the 6.5-fold variation (55-332 mg $C \cdot m^{-2} \cdot d^{-1}$) found in Fraser system lakes (Hume et al. 1996), but PR_{mean} averaged over all study lakes (109 mg $C \cdot m^{-2} \cdot d^{-1}$) was less than the overall average of 138 for Fraser system lakes (Shortreed et al. 1998). However, it was substantially more than reported for coastal British Columbia lakes, where the overall average of PR_{mean} was 70 (range: 44-106 mg $C \cdot m^{-2} \cdot d^{-1}$) (Stockner and Shortreed 1985).

AUTOTROPHIC PICOPLANKTON

In our study lakes, picoplankton abundance and community composition were similar to that reported in other western North American lakes. The range of 12,000-50,000/mL in seasonal average total numbers was within the wider range of 800-105,000/mL found in eleven lakes in British Columbia and the Yukon (Stockner and Shortreed 1991). In oligotrophic lakes, picoplankton numbers generally increase with increasing nutrient levels (Fahnenstiel et al. 1991;

Stockner and Shortreed 1991). In our study lakes highest picoplankton numbers occurred in Kitwanga and Morrison lakes, which had the highest PR_{mean}, chlorophyll, and TP (discounting Kitsumkalum Lake) concentrations. Stockner and Shortreed (1991) reported the highest proportion of colonial *Synechococcus* (CSYN) occurred in the more productive lakes, and in our study lakes the two most productive lakes (Kitwanga and Morrison) had the highest CSYN numbers. Eukaryotic picoplankton (REUK) have been found to be abundant only in acidic lakes (Soendergaard 1991; Stockner and Shortreed 1991). Data from this study confirms this low pH preference of REUK, since all study lakes were alkaline and REUK were present in low (<3%) numbers only. The red-fluorescing (phycocyanin) cyanobacteria RCYN was abundant only in Morrison Lake, which was humic-stained but not acidic. The only other B.C. lake RCYN has been found in abundance was a humic, acidic lake on the Queen Charlotte Islands (Stockner and Shortreed 1991). Pick (1991) suggested that light quality in highly colored lakes (particularly lakes with dissolved humic material) favored dominance by RCYN.

ZOOPLANKTON

Zooplankton are affected by "bottom-up" factors such as lake physics, chemistry, and lower trophic levels. In addition, higher trophic levels can have substantial "top-down" effects on the zooplankton community. The relative importance of "top-down" and "bottom-up" effects has been the subject of considerable research and discussion (Carpenter et al. 1985; Northcote 1988). In sockeye nursery lakes, these relationships can be extremely complex, particularly because sockeye are anadromous. Adult sockeye returning to spawn can bring substantial amounts of marine nutrients to their nursery lake (assuming they spawn in the lake or in tributaries flowing into the lake) (Stockner 1987). Emigrating smolts remove substantial amounts of nutrients from the lake. However, in most cases, nutrient output through smolt migration is a small (<5%) fraction of nutrient input from spawners or of nutrient output from discharge (Stockner 1987). Consequently, sockeye's anadromous life cycle most often results in a net increase in nutrient loading to a lake and increases its productivity.

During their freshwater residence, sockeye can also have a profound effect on nutrient cycling within a lake. Juvenile sockeye usually undergo diel vertical migrations where they spend daylight hours in the lake's hypolimnion and ascend at dusk to feed within the epi- or metalimnion (Levy 1990). Consequently, they remove (graze) plankton from the surface waters and recycle (excrete) nutrients to the deep waters where they are unavailable to the phytoplankton community. This is in direct contrast to planktivorous fish species which remain in the epilimnion and can be highly important nutrient recyclers (Northcote 1988). In addition, sockeye fry are size- and species-selective planktivores, so they can affect community composition as well as productivity. Juvenile sockeye selectively graze large cladocerans and, if available, will feed almost exclusively on *Daphnia* (Narver 1970; Goodlad et al. 1974; Morton and Williams 1990; Hume et al. 1996). High grazing pressure can shift zooplankton community structure from large bodied cladocerans to less productive, more predator-resistant species such as *Cyclops* and *Leptodiaptomus* (Brooks and Dodson 1965; Brooks 1968; Goodlad et al. 1974; Kyle et al. 1988).

In addition to grazing pressure, zooplankton production rates and community composition are strongly influenced by quantity and quality of available food (Wylie and Currie 1991; Guisande and Gliwicz 1992; Mitchell et al. 1992; Sterner et al. 1993; Rodriguez et al. 1995). Because of inefficient feeding strategies, under low food conditions (i.e. highly oligotrophic lakes), cladocerans are unable to obtain required energy for successful survival and reproduction, and copepods predominate (Gliwicz 1975; Allen 1976). Further, cladocerans such as *Daphnia* have relatively P-rich tissues, with atomic P/C ratios averaging 0.012 (they average only 0.005 in herbivorous copepods) (Sommer 1992). Consequently, when the relative P concentration in available food is low, *Daphnia* growth and reproductive rates are reduced, and copepods are usually dominant (Hessen 1990; Sterner and Hessen 1994). Even when food is abundant, if its C/P ratio is high, *Daphnia* exhibit reduced growth and reproductive rates (Mitchell et al. 1992; Sterner et al. 1993). In the majority of B.C. sockeye nursery lakes, low phytoplankton productivity is caused by P limitation (Stockner and Shortreed 1985), so low food quantity is accompanied by low food quality (high C:P ratios). In sockeye nursery lakes, predominance of copepods and small-bodied cladocerans may indicate high grazing pressure or may simply be a result of low phytoplankton food quality or quantity.

In our study lakes, the complexity of these relationships was clearly demonstrated. Photosynthetic rates (primary production) exhibited an 8-fold variation, zooplankton biomass varied 2 orders of magnitude, and planktivore biomass varied more than an order of magnitude. In addition, zooplankton community composition varied considerably between lakes. When planktivore grazing exerts little pressure on the zooplankton community, zooplankton biomass tends to be positively correlated with trophic status (Hanson and Peters 1984; Shortreed and Stockner 1986; Shortreed et al. 1996). In our study lakes, macrozooplankton biomass was significantly correlated with PR (r^2=0.83, n=6, Macrozooplankton biomass = 7.53 x PR - 247). However, because the relationship was driven by a single data point for Kitwanga Lake, the correlation was not significant (r^2=0.31, n=6) when data were log-transformed. Macrozooplankton biomass was not correlated with planktivore biomass (r^2=0.01, n=6, $p>0.05$). Further, planktivore density was <500/ha in most study lakes (Table 8). In sockeye nursery lakes elsewhere in B.C., planktivore densities of <500/ha did not have a detectable effect on plankton biomass or community composition (Hume et al. 1996). This suggests that with the exception of Alastair and Sustut lakes, planktivore biomass was not high enough in our study lakes for "top-down" control of the plankton community. Despite low planktivore densities, cladocerans were present in high numbers only in Kitwanga Lake, suggesting that the zooplankton communities in these lakes were food limited (bottom-up control).

ADULT SPAWNERS

There were no adult escapement estimates conducted for four of the lakes (Bear, Kitwanga, Morrison, and Swan) in the brood year we surveyed. For the purposes of this discussion, we used the average from the previous 10 years as an approximate escapement number for these four lakes. There was a significant relationship (r^2=0.95, $p<0.05$, n=8) between estimated numbers of female spawners and acoustic fall fry estimates (Fig. 32). This suggests that despite potential errors in accuracy, current escapement estimates provide a useful index of spawner numbers to the study lakes. In the brood year we surveyed, Johanson and Sustut lakes both had approximately 4 FS/ha. Alastair Lake has the highest spawner densities in the study, with an average of 5.1 FS/ha from 1985-1995 (4.7 FS/ha in the brood year we surveyed). Lakelse has averaged 2.0 FS/ha over the last 10 years and was 2.4 FS/ha for the brood year we surveyed. The remaining lakes had FS densities of <2.0 FS/ha. Even allowing for a substantial underestimate in escapement estimates to most study lakes, these densities are low compared to Fraser system lakes, where densities >20 FS/ha have been frequently observed and where density has little apparent effect on survival at densities <10 FS/ha (Hume et al. 1996).

JUVENILE FISH

Largest fall fry in our study lakes were from Bear, Lakelse, and Morrison lakes. Their size range of 3.9-6.1 g was similar to that seen in other productive B.C. sockeye lakes (McDonald and Hume 1984; Hume et al. 1996). Fall fry in the remaining lakes averaged <2.4 g, despite low planktivore densities in all lakes but Alastair. In an earlier study, Simpson et al. (1981) also reported that fall fry from Alastair and Swan lakes averaged <2 g. Age-0 fry in Morice Lake were <1 g, which probably contributes greatly to the high proportion of smolts which are age-2's. Analysis of scale samples from adult Morice Lake sockeye indicates that about 90% had spent 2 years in the lake (Bilton and Smith 1969; Shepherd 1979; Simpson et al. 1981). Among study lakes, there was no correlation between fall fry size and adult spawner density, most likely because other factors such as primary productivity, zooplankton abundance and community structure, and competitor numbers varied widely between lakes (Fig. 32).

In the shallower (mean depth<20 m) study lakes, we found highest densities of juvenile sockeye occurred in the deeper parts of the lakes. In B.C. lakes, juvenile sockeye most often spend the daylight hours at depths of 20-80 m (J. Hume, unpubl. data; Levy 1990, Levy et al. 1991). It has been hypothesized that this diel behaviour is a predator avoidance mechanism, since at these depths light levels are low enough that visual predators (piscivorous fish) cannot effectively detect prey (Henderson and Northcote 1985; Levy 1990). Sockeye normally spend the hours of darkness just below the thermocline (Narver 1970; Macdonald and Hume 1984). Shallow waters are often isothermal and when stratified, have a thermocline very near the bottom. Thus, even when actively feeding in shallow lakes, sockeye fry may be too close to the bottom to be detectable. In our shallow study lakes, it is possible that sockeye fry were present throughout the lake, but in shallower areas may have been too close to the bottom to be detected by the sounder. If this was the case, our acoustic data underestimated fry density. If the shallower areas of the lakes were not suitable habitat for sockeye and fry were not present in these locations, we again underestimated density because it was calculated using total lake surface area.

SOCKEYE DIET

Sockeye are selective planktivores, with the large-bodied cladoceran *Daphnia* spp. a preferred food source. When it is present in sufficient numbers, juvenile sockeye will feed almost exclusively on *Daphnia* (Narver 1970; Goodlad et al. 1974; Morton and Williams 1990; Hume et al 1996). *Heterocope* is a large calanoid copepod which is less common than *Daphnia*, but when available is also preyed on actively (Narver 1970; Goodlad et al. 1974). *Diacyclops*, *Leptodiaptomus*, and small bosminids are heavily utilized only when numbers of preferred food items are very low. Their utilization is indicative of high grazing pressure and/or extreme oligotrophy. Interpretation of sockeye diet data in this study is confounded to some degree because data are only available from fall samples (late summer from Johanson and Sustut lakes). Stomach contents and fullness depends to a large extent on seasonality within the zooplankton community and by fall preferred food items can be reduced to low numbers, even though they have been a major food source for much of the summer. However, if preferred food items are present in substantial numbers in fall stomach samples, an ample food supply and density-independent growth are strongly suggested.

Juvenile sockeye stomachs from Kitwanga, Lakelse, and Swan lakes were >75% full and contained mostly *Daphnia*, indicating that juvenile sockeye had abundant prey and were not present in sufficient numbers to adversely affect the zooplankton community (Fig. 30). However, despite a high quality food source, a good physical environment (Stockner and Shortreed 1979), and low planktivore densities, Swan Lake fall fry averaged only 1.3 g. Abundant *Daphnia* and small fry were also found in a 1978 study of Swan (Simpson et al. 1981; Rankin et al. 1984). At this time we cannot explain the low growth rates of Swan Lake sockeye, but one possibility is that most fry caught in the trawl were age-0 kokanee, which are smaller than age-0 sockeye in some lakes (Wood et al. 1998). In Bear Lake, juvenile sockeye stomachs were 60% full and contained *Daphnia* and the large-bodied calanoid copepod *Heterocope*. At present densities, growth and survival of Bear Lake juvenile sockeye do not appear to be limited by the food supply. In Morrison Lake, sockeye stomachs were 50% full and contained mostly calanoid copepods (*Epischura* and *Leptodiaptomus*). *Epischura* is not a common dietary item of juvenile sockeye, but it is large enough to be an effective food source. Sockeye stomachs from Alastair, Johanson, Morice, and Sustut lakes were <30% full and contained bosminids and small copepods, a diet which is suggestive of high grazing pressure and/or extreme oligotrophy. However, low sockeye densities in these lakes indicates "bottom up" rather than "top down" control of the zooplankton community.

COMPETITORS AND PREDATORS

Since adult kokanee have been found in Bear, Johanson, Kitwanga, Morrison and Swan lakes (MOELP, data on file), an unknown proportion of the age-0 *O. nerka* we captured were presumably kokanee. Other species of limnetic planktivores (including stickleback and whitefish) were found in all lakes except Johanson, Kitsumkalum, and Morice. These included stickleback, whitefish and older age classes of sockeye. In most lakes, density of fish other than age-0 sockeye was low (<200/ha), but they comprised up to one-third of the total limnetic fish population in Morrison and Lakelse lakes and over one-half in Bear Lake. Stickleback density in Alastair Lake was >4,200/ha, 2x greater than sockeye density. In some lakes, stickleback compete strongly with age-0 sockeye (O'Neill and Hyatt 1987). In Alastair Lake, there was considerable overlap in the diet of the two species (sockeye ate bosminids almost exclusively and bosminids comprised about 50% of stickleback diet), so there appears to have been substantial competitive interaction. The mysid *Neomysis mercedis* occurred in Lakelse Lake, where it was most abundant in the shallower parts of the lake (primarily near the outlet). Mysids can compete with juvenile sockeye (Murtaugh 1981a, 1981b, 1984) and when abundant may effectively reduce a lake's juvenile sockeye rearing capacity.

Predation can have significant effects on the survival, growth, and behaviour of juvenile sockeye salmon (Parkinson et al. 1989; Beauchamp et al. 1995, 1997). All study lakes contained fish species which are potential predators of juvenile sockeye, including burbot (*Lota lota*), cutthroat trout (*O. clarki*), Dolly Varden (*Salvelinus malma*), lake trout (*S. namaycush*), rainbow and steelhead trout (*O. mykiss*), and northern squawfish (*Ptychocheilus oregonensis*) (Table 9). Although abundance estimates are not available, direct evidence of predation on sockeye is available for several of the study lakes. Brett and Pritchard (1946b) observed cutthroat trout and Dolly Varden feeding on migrating sockeye smolts in Lakelse Lake. In Morice Lake, Brett and Pritchard (1946a) found that 50% of the stomach contents of lake trout consisted of age-0 and age-1 salmon. Dolly Varden and rainbow trout from Swan Lake contained 30 and 20% sockeye fry by volume, respectively (Withler 1948).

REARING CAPACITY

We used the PR model (Hume et al. 1996; Shortreed et al. 1998) to predict rearing capacity, optimum escapements, and maximum smolt production for the study lakes (Table 10). The model and its assumptions have been discussed in detail elsewhere (Shortreed et al. 1998). The PR model assumes negligible numbers of planktivorous fish other than age-0 juvenile sockeye. If competitive planktivores are present in sufficient numbers (as is the case in several of the study lakes), the PR model overestimates the lake's juvenile sockeye rearing capacity and optimum escapement. To compensate for the presence of these planktivores, we adjusted PR model predictions downwards by subtracting the biomass of species other than sockeye from predicted maximum smolt biomass. Predicted optimum escapement was adjusted by the same proportion. In these modified PR model predictions, we assumed that the biomass of non-sockeye would remain constant with increasing sockeye escapements. In lakes with age-1 juvenile sockeye, we assumed that the proportion of age-0 and age-1 sockeye would remain the same with increasing escapements, and adjusted predictions downward by the relative proportion of age-0 and age-1 sockeye biomass. PR model predictions of sockeye production from the study lakes were reduced by negligible amounts in some lakes and by up to one-third in others (particularly Alastair and Morrison lakes) (Table 10).

Another assumption in PR model predictions of optimum escapements is that lake rearing capacity and not spawning ground capacity limits smolt production. However, some B.C. lakes (including some lakes in this study) have less spawning ground capacity than lake rearing capacity. In these cases, the PR model produces excessive predictions of optimum escapement, and is most useful in estimating the amount of enhancement (e.g. spawning channel construction, fry outplants) that is biologically feasible. Spawning habitat of Skeena system lakes is poorly defined, with few estimates available except for a study done in the 1940's (Brett 1952), which provided estimates of available spawning ground area for all study lakes except Johanson and Morrison. More recently, Simpson et al. (1981) corroborated Brett's estimate of stream spawning ground area for Swan Lake. We estimated spawning ground capacity for each lake by assuming an optimum spawning ground density of 1.0 female/m^2 (West 1987) (Table 11).

However, these estimates do not include lake spawning capacity, which has been observed in Bear, Kitsumkalum, Kitwanga, Sustut, and Swan lakes. It is also probable that lake spawning occurs in some or all of the remaining study lakes.

To compare lake rearing capacity with spawning ground capacity, we needed to make a number of assumptions about the latter. If lake spawning was observed, we arbitrarily assumed that spawning capacity was 2x Brett's (1952) estimate. No data are available for Kitwanga Lake, but because of its sometimes unfavorable physical environment for rearing sockeye, we recommended an optimum escapement one-third that of the PR model. No data on spawning ground capacity of Morrison Lake or its tributaries are available other than Brett's (1952) statement that spawning capacity of the major tributary was limited. However, Morrison Lake is an effective sockeye nursery area and we assumed that spawning ground capacity was one-half lake rearing capacity (Table 11).

Recommended escapements are based on rearing capacity and spawning capacity, whichever is smaller (Table 11). In our study it was not possible to verify estimates of spawning ground capacity, but they are most likely underestimates because they do not include lake spawning capacity. It is important to recognize that our recommended escapement targets are our best estimate of the actual number of spawners required to fully utilize available capacity (lake or spawning, whichever is limiting). Current visual survey methods of estimating escapements must be adjusted as necessary to correct for underestimation bias before comparing current escapements with our recommended escapements. Recent average estimated escapements (1985-1995) range from 8-35% of our recommended escapements (Table 11). Despite recent escapement increases to several of the study lakes (e.g. Johanson, Kitsumkalum, Morice, Sustut and Swan), current spawning densities are low relative to our recommended escapements, even after allowing that escapement estimates from visual surveys may seriously underestimate actual numbers. Despite the inadequacies of some of the data used for these estimates (and the assumptions made), we conclude that the current production of sockeye from non-Babine Skeena system lakes is less than 25% of its potential, given optimum spawning escapements (Table 11).

LAKE SUMMARIES AND RECOMMENDATIONS.

Alastair Lake

Alastair Lake has a suitable physical environment for juvenile sockeye, with a mean depth of 24 m and deep water (>50 m) in the southern end. With a mean surface temperature of 14°C, a 10-m deep thermocline, and a cool hypolimnion, its thermal regime is favorable for sockeye. The lake is relatively clear, with an average euphotic zone depth (13.5 m) slightly greater than the thermocline. The lake is very productive and has one of the three highest photosynthetic rates ever recorded for B.C. sockeye lakes. Juvenile sockeye were distributed throughout the lake. Alastair has high densities (>6,200/ha) of limnetic fish (this is an underestimate because of limitations of echo counting at these high densities), of which 2/3 are stickleback and the remainder are sockeye. Growth rates of juvenile sockeye are low (they weighed an average of only 1.7 g in October), most likely because of intense competition from the large numbers of stickleback. Sockeye stomachs were only 20% full and contained nearly

100% *Bosmina*, a lower quality food item. Although the observed mean escapements are only 24% of recommended escapement, successful enhancement of Alastair Lake sockeye will require a reduction in stickleback numbers. This would allow the production of larger, less-predator resistant zooplankton species, which would most likely increase growth and reduce mortality of age-0 sockeye fry.

Bear Lake

Bear lake has a mean depth of 14 m, an average thermocline depth of 7 m, and a mean surface temperature of 14.6°C. It has areas of deep water (35-70 m) for much of its length. The average euphotic zone depth is only slightly greater than the thermocline depth. It is one of the 3 most productive lakes in this study. Limnetic fish densities were low and were made up of about equal densities of sockeye and whitefish. Sockeye stomachs were 60% full and contained mostly *Daphnia* and *Heterocope*, which are large and desirable food items. As a result, fall fry were large (4 g). PR model predictions indicate that current juvenile sockeye biomass is <10% of the biomass which the lake could produce (Table 11). Increased fry recruitment through management of the fishery (i.e. increased escapements) or fry stocking is needed to enhance this population.

Johanson Lake

Johanson Lake has a cool, relatively deep (10 m) epilimnion and a mean depth of 16 m. Areas of the lake are up to 40 m deep. The lake's high elevation (1,400 m) results in a short growing season (isothermal conditions last until late June). Euphotic zone depths were the deepest of any lake in the study. The lake is ultra-oligotrophic, with low nutrient concentrations and low PR. Together with Sustut Lake, Johanson had the lowest zooplankton biomass of any lake in the study. Most common zooplankton were small bosminids. Sockeye stomachs were only 25% full and contents consisted mainly of insects. Limnetic fish densities were low and were almost exclusively sockeye fry. Age-1 sockeye, which made up 10% of the population, had an average size of 2.4 g, which was smaller than age-0 sockeye in some of the more productive Skeena lakes. While data indicate that increased fry recruitment would increase smolt production from Johanson Lake, the lake's short growing season and ultra-oligotrophic status make it a less than ideal rearing environment. Lake fertilization would increase productivity and increase the available food supply for juvenile sockeye.

Kitsumkalum Lake

Kitsumkalum Lake provides a good physical habitat for sockeye fry, with a cool, deep epilimnion and an extensive hypolimnion. However, the lake is glacially turbid, with an average euphotic zone depth of only 3.8 m. Since the average thermocline depth was 25.5 m, primary productivity is limited by light availability. Although total phosphorus could not be measured, total dissolved solids were the lowest of any lake in the study, suggesting low nutrient loading as well as a poor light climate. As a result, Kitsumkalum had the lowest productivity of any B.C. sockeye nursery lake for which we have data. Zooplankton biomass was low and consisted mainly of diaptomid copepods. Sockeye stomachs were only 20% full and contained mainly diaptomids and some *Daphnia*. Despite low densities, fall sockeye fry averaged only 1.6 g. The lake provides a relatively poor rearing environment but sockeye numbers are currently well below optimum (Table 11) and increasing escapements would most likely increase subsequent smolt production. Because of its turbidity, lake fertilization is not a viable enhancement option.

Kitwanga Lake

Kitwanga is the shallowest lake in this study, with a mean depth of only 5 m and a maximum depth of 15 m. It has a prolonged period of strong thermal stratification with a thermocline depth of 5.7 m. Because the lake is shallow, portions of the lake are isothermal in summer, and its hypolimnion is much smaller than its epilimnion. For 4-6 weeks in mid-summer, epilimnetic temperatures exceed 18°C. Where a hypolimnion does exist, summer oxygen concentrations may become depleted. Thus, there may be no daytime cold-water refuge for sockeye and epilimnetic temperatures are above the optimum for growth and predation avoidance. The lake is relatively clear and the euphotic zone encompasses the entire water column in most areas of the lake. Kitwanga is one of the most productive sockeye nursery lakes in B.C. Macrozooplankton biomass is high and is comprised mainly of *Daphnia*. In fall, juvenile sockeye averaged only 2.4 g despite low limnetic fish density and the abundant prey. However, only 4 sockeye were caught in our trawls and some or all may have been kokanee. Present and historic sockeye production from Kitwanga Lake is far below the optimum predicted by the PR model (Table 11). Further work is needed to define the factors limiting sockeye production in this system. These factors could include recruitment limitation, spawning ground limitation, and unfavorable limnological conditions.

Lakelse Lake

The southern end of Lakelse Lake is <6 m deep, but the northern half of the lake has a large area >20 m in depth. While its epilimnion is relatively deep (13.5 m) for a lake of this size, there is a coldwater refuge area for juvenile sockeye in the southern end of the lake. With an average depth of 7.7 m, the euphotic zone is slightly more than one-half the epilimnion depth and comprised the entire water column in the northern part of the lake. Consequently, littoral production may be an important component in sockeye growth. The limnetic zone of the lake is oligotrophic and has an extended summer period of epilimnetic nutrient depletion. Since the surface mixed layer extends to the lake bottom for a large proportion of the lake, recycling from the sediments may be a substantial source of nutrients during this period. *Daphnia* were present in sufficient numbers to be a readily available food source and juvenile sockeye stomachs were full, with *Daphnia* comprising >90% of their diet. Sockeye densities were low, as were numbers of stickleback. At an average size of 6 g, Lakelse fall fry were the largest in this study and among the largest found in British Columbia. Sockeye fry biomass was 51% of the PR model's prediction of maximum production and recent escapements have averaged 15% of predicted optimum escapements (Table 11). Increased fry recruitment through increased escapements (fishery management) or fry stocking would be the best ways to enhance this population.

Morice Lake

Morice Lake has generally excellent physical conditions for juvenile sockeye, with clear water, a cool epilimnion, and a large hypolimnion. However, as a result of very low nutrient loading, Morice is ultra-oligotrophic. Despite low planktivore densities, zooplankton biomass is relatively low, resulting in slow growth rates for sockeye fry. Age-0 fall fry were the smallest (0.8 g) of any lake in the study. Sockeye stomachs were <30% full and contained mostly bosminids, a less than ideal food source which in this case indicates extreme oligotrophy. The large proportion of 2-year old smolts in Morice is also indicative of its low productivity. Adult sockeye escapements to Morice Lake are currently well below predicted optimum escapements and further escapement increases would no doubt produce additional smolts. However, lake fertilization in conjunction with increased fry recruitment would be the most effective restoration technique. It would increase fry growth rates and would possibly increase productivity of Morice sockeye by reducing the proportion of age-2 smolts.

Morrison Lake

Morrison Lake provides a good physical habitat for sockeye fry with a mean depth of 21 m and a mean epilimnetic temperature of 13.5°C. It has a relatively shallow mean thermocline depth of 6.2 m and its organic stained water results in an average euphotic zone depth of only 4.2 m. The lake is oligotrophic but total phosphorus concentration is higher than any study lake except Kitwanga. Phytoplankton biomass (chlorophyll) is second only to that in Alastair Lake but because of the rapid light attenuation, mean daily photosynthetic rate is about average for the study lakes. Calanoid copepods (predominantly *Epischura* sp.) were the main prey item found in sockeye stomachs, which were 45% full. These data could be misleading, because by the October 29 survey date the growing season was nearly over and all zooplankton were at low levels. The large size (4.3 g) of age-0 fall fry indicates an ample food resource during the growing season. Sockeye densities were low, as were numbers of other limnetic species, which consisted primarily of whitefish but also included redside shiners and sculpins. Total sockeye biomass was 39% of the maximum predicted by the PR model. Recent escapements are <30% of our recommended escapements. Increased fry recruitment through increased escapements or fry stocking would be the most effective way to enhance/restore this stock.

Sustut Lake

Sustut Lake is one of the shallowest lakes in the study, with a mean depth of 6 m and a maximum depth of only 19 m. Like Johanson Lake, Sustut is situated at a high elevation and as a result has a cool epilimnion (mean surface temperature=13°C) and a short growing season. Its thermocline is unstable for much of the growing season. While the cool temperature of the surface mixed layer may compensate to some degree, the lack of a cold, hypolimnetic refuge results in temperatures higher than optimal for sockeye growth. The euphotic zone extends to the lake bottom in most areas of the lake. Total phosphorus levels are relatively high but the lake has a severe nitrogen deficiency throughout the growing season. With Johanson Lake, Sustut had the lowest macrozooplankton biomass of all study lakes. Sockeye stomachs were only 25% full and contained mostly bosminids. Compared to most other study lakes, limnetic fish densities were high and were almost exclusively age-0 sockeye. Fry were small, but the August sampling date makes it difficult to compare to other lakes. Total juvenile sockeye biomass was about 62% of the optimum predicted by the modified PR model and recent observed escapements have been 30-50% of our recommended optimum levels. Increasing fry recruitment to Sustut Lake may increase smolt production, but the most effective enhancement would be combining increased recruitment with lake fertilization.

Swan Lake

Swan Lake is near the mid-range of productivity for the study lakes. Its physical environment is excellent, with clear water, a cool epilimnion, and a large hypolimnion. *Daphnia* are fairly abundant throughout the growing season and sockeye stomachs were >75% full, with *Daphnia* making up most of the stomach contents. Planktivore densities were relatively low, but they were higher than any other study lake except Alastair, Morrison, and Sustut. However, despite a good physical environment, an abundant food supply, and low planktivore densities, Swan Lake fall fry averaged only 1.3 g. At this time it is unclear why this is the case. While increasing fry recruitment would most likely increase smolt production, it would not be prudent to invest in any enhancement technique such as fry stocking or fertilization until reasons for the small fry size are understood.

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Table 1. Geographic and morphometric data from the study lakes.

Lake	Latitude (°N)	Longitude (°W)	Elevation (m)	Surface area (km^2)	Drainage basin area (km^2)	Mean depth (m)
Alastair	54°06'	129°11'	30	6.9	85	24
Bear	56°06'	126°49'	805	19	353	14
Johanson	56°35'	126°11'	1,444	1.4	41	16
Kitsumkalum	54°47'	128°47'	122	18	1,755	81
Kitwanga	55°22'	128°07'	376	7.8	169	5
Lakelse	54°23'	128°33'	137	13	360	8
Morice	54°00'	127°40'	764	96	1,873	69
Morrison	55°14'	126°22'	730	13	450	21
Sustut	56°35'	126°27'	1,301	2.5	68	6
Swan	56°46'	128°39'	525	17	118	23

Table 2. Variation in salient physical variables in the study lakes. All data are seasonal averages. Data on Alastair, Bear, Morice, and Swan lakes are from Stockner and Shortreed (1979).

Lake	Year	Surface temp. (°C)	Mean epil. temp. (°C)	Secchi depth (m)	Thermocline depth (m)	EZD (m)	Ext. coeff. (/m)
Alastair	1978	14.0		4.8	10.4	13.5	0.40
Bear	1978	14.6		5.2	7.2	8.8	0.56
Johanson	1994	11.7	8.3	10.2	10.0	21.4	0.19
Kitsumkalum	1994	12.5	11.0	0.9	25.5	3.8	1.10
Kitwanga	1995	16.2	14.7	6.7	5.7	11.6	0.37
Lakelse	1994	16.8	16.0	4.6	13.5	7.7	0.55
Morice	1978	10.2		5.6	25.8	19.8	0.32
Morrison	1995	15.5	13.5	2.9	6.2	4.2	0.87
Sustut	1994	12.8	11.1	9.7	4.5	15.1	0.28
Swan	1978	13.2		7.6	9.6	15.3	0.32

Table 3. Variation in chemical data from the study lakes. Data on Alastair, Bear, Morice, and Swan lakes are from Stockner and Shortreed (1979), except for total P data from Morice Lake, which are from Costella et al. (1982).

Lake	Year	pH	T.D.S. (mg/L)	Total alk. (mg $CaCO_3$/L)	Silicate (mg Si/L)	Nitrate (µg N/L)	Total P (µg/L)
Alastair	1978		32		0.23	2.8	
Bear	1978		41	20.2	1.52	2.1	
Johanson	1994	7.16	52	19.6	1.74	1.9	3.3
Kitsumkalum	1994	7.15	28	15.1	1.21	35	14.0[a]
Kitwanga	1995	7.46	68	59.5	1.71	1.5	7.4
Lakelse	1994	7.33	47	21.6	1.71	8.1	5.4
Morice	1978	7.00	36	13.0	1.04	31	2.0
Morrison	1995	7.13	60	26.4	2.03	10	6.9
Sustut	1994	7.28	52	26.3	2.25	0.8	6.5
Swan	1978		29	13.5	0.72	8.1	

[a] - high because of glacial turbidity.

Table 4. Variation in seasonal averages of particulate elements and salient atomic ratios. Morice Lake data are from Costella et al. (1982).

		Part. mass (µg/L)			Part. ratio (by atoms)		
Lake	Year	C	N	P	C/N	C/P	N/P
Alastair	1978						
Bear	1978						
Johanson	1994	261	25	2.0	12.2	340	28
Kitsumkalum	1994	239	22		12.7		
Kitwanga	1995	348	41	3.0	10.0	302	30
Lakelse	1994	313	35	3.7	10.5	217	21
Morice	1980	187	28		5.5		
Morrison	1995	354	40	3.4	10.3	273	26
Sustut	1994	373	36	4.1	12.1	237	20
Swan	1978						

Table 5. Variation in seasonal averages of salient biological variables from the study lakes. Data on Alastair, Bear, Morice, and Swan lakes are from Stockner and Shortreed (1979), except for bacteria data from Morice Lake, which are from Costella et al. (1982). Macrozooplankton are zooplankton >250 µm.

Lake	Year	Bacteria ($\#x10^6$/mL)	Chlorophyll (µg/L)	Daily PR (mg C/m^2)	Phytoplankton $\#x10^3$/mL			Macrozooplankton Biomass (mg/m^2)
					Pico.	Nano.	Micro.	
Alastair	1978		2.74	209				
Bear	1978		1.75	144				
Johanson	1994	0.64	0.97	66	27.38	0.26	0.64	17
Kitsumkalum	1994	1.04	0.60	33	11.90		0.13	97
Kitwanga	1995	1.92	1.53	265	45.28	0.69	1.11	1770
Lakelse	1994	0.94	1.38	74	22.93	0.76	0.57	718
Morice	1980	0.67	0.79	65				
Morrison	1995	1.28	2.32	108	50.78	1.53	0.94	678
Sustut	1994	1.15	1.43	88	38.30	0.44	3.97	17
Swan	1978		0.92	93				

Table 6. Variation in average biomass of major zooplankton groups. Bosminidae are primarily *Eubosmina longispina*, Cyclopidae are mainly *Cyclops scutifer* with some *Diacyclops thomasi*, and Diaptomidae are *Leptodiaptomus ashlandi* and *L. pribilofensis*.

Lake	Year	Zooplankton biomass (mg dry wt/m^2)							
		Bosminidae	Cyclopidae	Diaptomidae	*Daphnia*	*Heterocope*	*Epischura*	*Holopedium*	*Diaphanosoma*
Johanson	1994	12	3.5	0.1	0.5	0	0.0	0.3	0.0
Kitsumkalum	1994	0.1	12	83	0.1	0	0.2	0.0	0.0
Kitwanga	1995	0.4	504	149	1113	0	0.8	0.0	0.9
Lakelse	1994	48	482	19	66	0	64	0.0	36
Morrison	1995	15	192	351	13	94	4.6	1.6	2.5
Sustut	1994	12	1.3	0	2.6	0	0.0	0.0	0.0

Table 7. Mean size and length of trawl caught fish from the study lakes.

		Catch		Weight (g)					Length (mm)				
Lake	Dates	Taxa	N	Mean	95% CI	SD	Min	Max	Mean	95% CI	SD	Min	Max
Alastair	Oct 11-12/95	age-0	324[a]	1.7	0.09	0.79	0.57	4.62	54	0.8	7.5	38	75
		stickleback	364	1.19	0.06	0.57	0.12	3.55	49	0.9	8.9	26	69
Bear	Oct 3-4/95	age-0	9	3.89	2.37	3.09	1.35	10.34	64	11.7	15.2	48	92
		bull trout	1	1.94			1.94	1.94	56			56	56
		rainbow trout	1										
		redside shiner	1										
		whitefish	17										
Johanson	Aug 25/95	age-0	30	0.88	0.11	0.29	0.32	1.56	43	1.8	4.9	35	55
		age-1	20	2.41	0.17	0.37	1.81	3.03	63	1.6	3.4	57	69
Kitsumkalum	Oct 8/94	age-0	114	1.61	0.12	0.65	0.53	3.87	53	1.4	7.3	33	72
		river lamprey	1	3.53			3.53	3.53	134			134	134
Kitwanga	Oct 9-10/95	age-0	4	2.36	1.18	0.74	1.58	3.17	59	11.7	7.4	52	67
		sucker	1										
Lakelse	Oct 9/94	age-0	82	6.12	0.34	1.56	1.57	9.17	80	1.6	7.3	54	91
		stickleback	8	0.35	0.11	0.13	0.2	0.51	34	3.6	4.3	27	39
		river lamprey	3	0.9	1.52	0.61	0.44	1.59	80	45.1	18.2	65	100
Morice	Sept 24-25/93	age-0	42	0.82	0.06	0.19	0.5	1.47	45	1	3.2	39	55
		age-1	2	6	12.71	1.41	5	7	82	44.5	4.9	78	85

Table 7 (continued). Mean size and length of trawl caught fish from the study lakes.

		Catch		Weight (g)					Length (mm)				
Lake	Dates	Taxa	N	Mean	95% CI	SD	Min	Max	Mean	95% CI	SD	Min	Max
Morrison	Sept 29/95	age-0	39[b]	4.29	0.63	1.8	0.75	8.57	70	3.6	10.2	42	90
		redside shiner	1										
		sculpin	2										
		unknown	4										
		whitefish	5	5.78	3.07	2.48	3.18	8.83	81	14.5	11.6	68	93
		whitefish	2										
Sustut	Aug 23-24/94	age-0	195	0.96	0.07	0.51	0.16	3.23	43	1	7.1	28	65
		whitefish	1	1.98			1.98	1.98	58			58	58
		Cyprinid	42	1.69	0.72	0.5	1.33	2.04	51	9.1	6.4	46	55
Swan	Oct 7-8/95	age-0	18	1.33	0.12	0.23	0.95	1.84	50	1.6	3.2	45	57

[a] - 4 age-0 sockeye not measured.
[b] - 5 age-0 sockeye not measured.

Table 8. Estimated female sockeye spawners, acoustic population estimates and biomass for age-0 sockeye and other major midwater fish species in the study lakes.

Lake	Brood year	Female spawners Total	#/ha	Date of survey	Acoustic method	Species	Population (N)	Density (N/ha)	95%CI	Biomass (kg/ha)
Alastair	1994	3,250	4.71	Oct.11, 1995	Echo Count	age-0	1,373,073	1,994	45%	3.39
						stickleback	2,871,912	4,171	25%	4.96
Bear	1994	1,183	0.63[a]	Oct.1, 1995	Echo Count	age-0	251,231	132	70%	0.36
						whitefish	340,823	180	46%	
Johanson	1993	511	3.65	Aug.25, 1994	Echo Count	age-0	44,900	357	102%	0.28
						age-1	5,051	36	73%	0.09
Kitsumkalum	1993	1,850	1.00	Oct.8, 1994	Integration	age-0	230,569	125	66%	0.20
						lamprey	6,024	3	64%	
Kitwanga	1994	675[a]	0.87[a]	Oct.9, 1995	Echo Count	age-0	59,455	77	94%	0.18
						other	3,452	4	180%	
Lakelse	1993	3,200	2.37	Oct.9, 1994	Integration	age-0	420,227	311[c]	53%	1.90
						stickleback	119,660	89[c]	40%	0.03
Morice	1992	13,500	1.41	Sep.24, 1993	Integration	age-0	649,420	86	38%	0.06
						age-1	176,086	18	84%	0.11
Morrison	1994	3,078	2.33[a]	Oct.29, 1995	Echo Count	age-0	497,473	377	31%	1.62
						other[b]	194,699	147	26%	0.85
Sustut	1993	1,085	4.34	Aug.23, 1994	Echo Count	age-0	444,828	1,779	64%	1.58
						cyprinids	3,405	14	90%	
Swan	1994	4,181	2.39[a]	Oct.6, 1995	Echo Count	age-0	824,777	475	50%	0.63
						other	38,391	22	63%	

[a] - Mean of previous 10 years. Adult spawners were not enumerated in 1994.
[b] - This is redside shiners, sculpins, and whitefish combined.
[c] - Scaling this data by the conversion factor of 1.65 found by Parkinson et al. (1994) would elevate the estimate to approximately 500 age-0 sockeye/ha and 150 stickleback/ha.

Table 9. Potential predator fish species found in the study lakes.

Lake	Burbot	Cutthroat	Dolly Varden	Lake trout	Rainbow	Squawfish	Steelhead
Alastair[1]		x	x		x		
Bear[2]	x	x		x	x		
Johanson[3]			x				x
Kisumkalum[4]		x	x				
Kitwanga[5]		x	x		x	x	
Lakelse[6]		x				x	
Morice[7]	x			x			
Morrison[8]	x	x		x	x	x	
Sustut[3]	x		x				x
Swan[9]			x	x			

[1]Data on file - Ministry of Environment, Fisheries Branch, Vancouver, B.C., [2]Foskett (1947b), [3]Foskett (1947a), [4]Brett (1946), [5]McConnell and Brett (1946), [6]Pritchard and Brett (1946b), [7]Pritchard and Brett (1946a), [8]McMahon (1948), [9]Withler (1948).

Table 10. PR model predictions of optimum escapements (total spawners), and maximum smolt production from Skeena system lakes. Modified PR predictions were calculated by reducing PR predictions of maximum biomass by the biomass of planktivorous fish which were not age-0 sockeye.

		PR model predictions			Modified PR model predictions		
Lake	Annual PR (t C/lake)	Optimum escapement (thousands)	Smolt biomass (tonnes)	Smolt number (millions)	Optimum escapement (thousands)	Smolt biomass (tonnes)	Smolt number (millions)
Alastair	252	47	12	2.6	34	8.4	1.8
Bear	491	92	23	5.0	85	21.1	4.6
Johanson	17	3	0.8	0.2	2	0.6	0.1
Kitsumkalum	109	20	5	1.1	20	5.1	1.1
Kitwanga	401	75	19	4.1	75	18.6	4.1
Lakelse	210	39	10	2.1	39	9.7	2.1
Morice	1,128	211	52	11.4	137	34.1	7.4
Morrison	255	48	12	2.6	44	10.9	2.4
Sustut	29	5	1.4	0.3	5	1.3	0.3
Swan	294	55	14	3.0	55	13.7	3.0

Table 11. Comparison of optimum escapement estimates, spawning ground capacity, recommended escapements, and observed escapements to the study lakes. All numbers are in thousands.

Lake	Opt. esc. from modified PR model	Spawning ground capacity[a]	Recommended optimum escapement[e]	Observed escapements: Mean 1985 -1995	Mean as % of Recom.	Maximum 1985 -1995	Maximum 1950 -1995
Alastair	34[h]	37	30[h]	7.1	24%	11.0	44.0
Bear	85	16+	30	2.6	9%	5.0	16.2
Johanson	2.3	na[b]	2	0.8	40%	2.6	2.6
Kitsumkalum	20	42+	20	2.8	14%	5.5	5.5
Kitwanga	75	+	25	1.4	6%	2.2	2.2
Lakelse	39	95	40[f]	6.0	15%	16.8	40.5
Morrison	44	little[c]	20	5.7	29%	14.7	24.2
Sustut	5.4	+	5	1.3	26%	2.6	3.0
Swan	55	15[d]+	30	8.1	27%	13.1	13.1
Total	359.7	>204	200[g]	35.8	18%	73.5	151.3
Morice	137	116.3	110	14.6	13%	40.0	55.4

[a] Total spawner numbers, stream spawning ground area (Brett 1952), and 1.0 m^2/spawning pair (West 1987).
[b] Johanson Lake was not included in Brett's (1952) summary.
[c] Brett (1952) reported that Tahlo Cr. had very limited and scattered spawning grounds.
[d] Includes Upper Club Creek.
+ Indicates observed but unknown amount of lake spawning habitat.
[e] Recommended escapements are based on the modified PR model and spawning ground capacity. If lake spawning was observed, we arbitrarily assumed that spawning capacity was 2x Brett's (1952) estimate. No data are available for Kitwanga Lake, but because of its sometimes unfavorable physical environment, we recommended an optimum escapement one-third that of the PR model.
[f] Lakelse Lake contains *Neomysis mercedis*, which may compete with juvenile sockeye. Since we do not know if this competition occurs in Lakelse and since we did not obtain an estimate of *N. mercedis* biomass, we did not adjust the recommended optimum escapement.
[g] Not equal to sum of the tabled data because of rounding error.
[h] These overestimate optimum escapement because of underestimated stickleback numbers.

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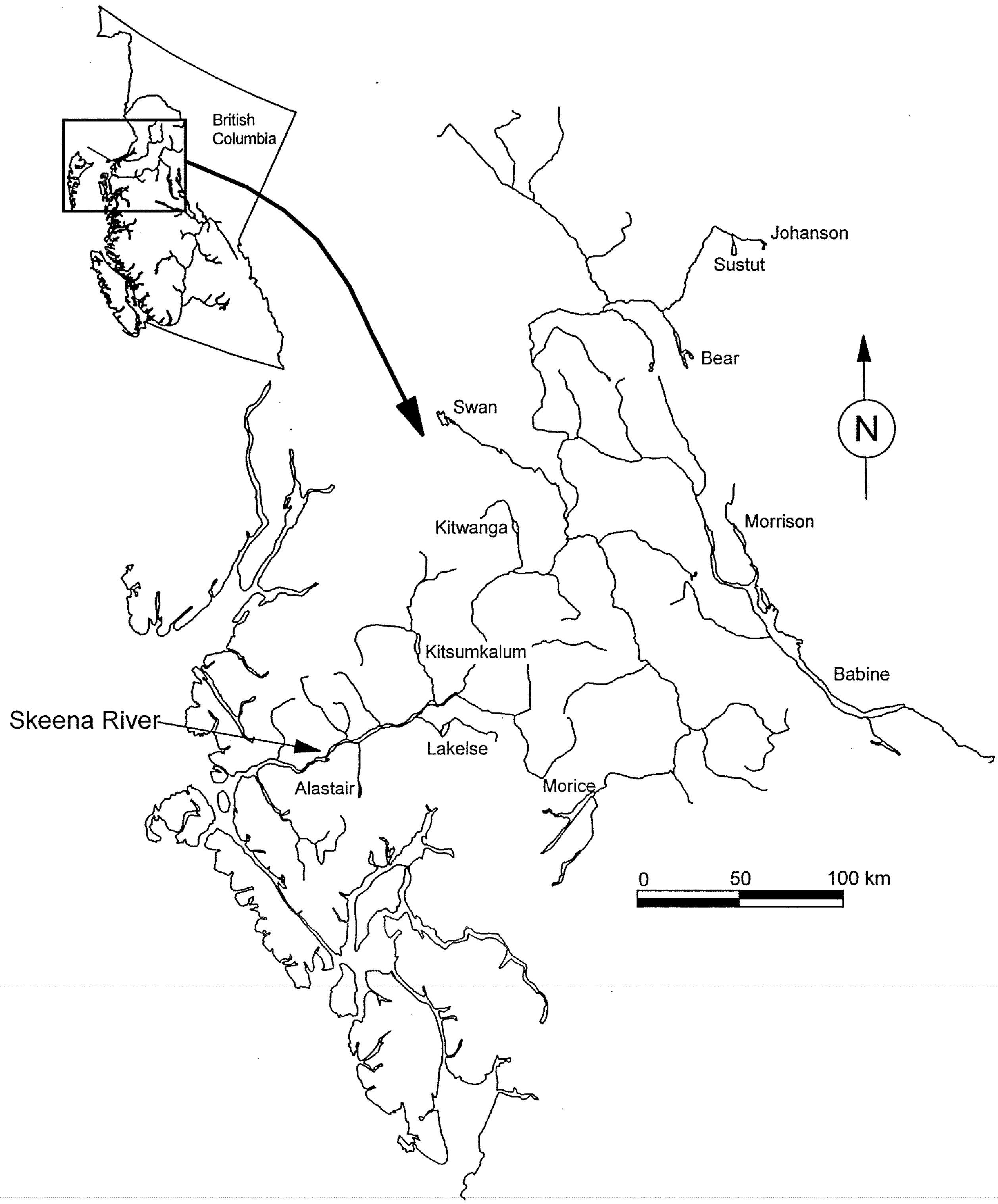
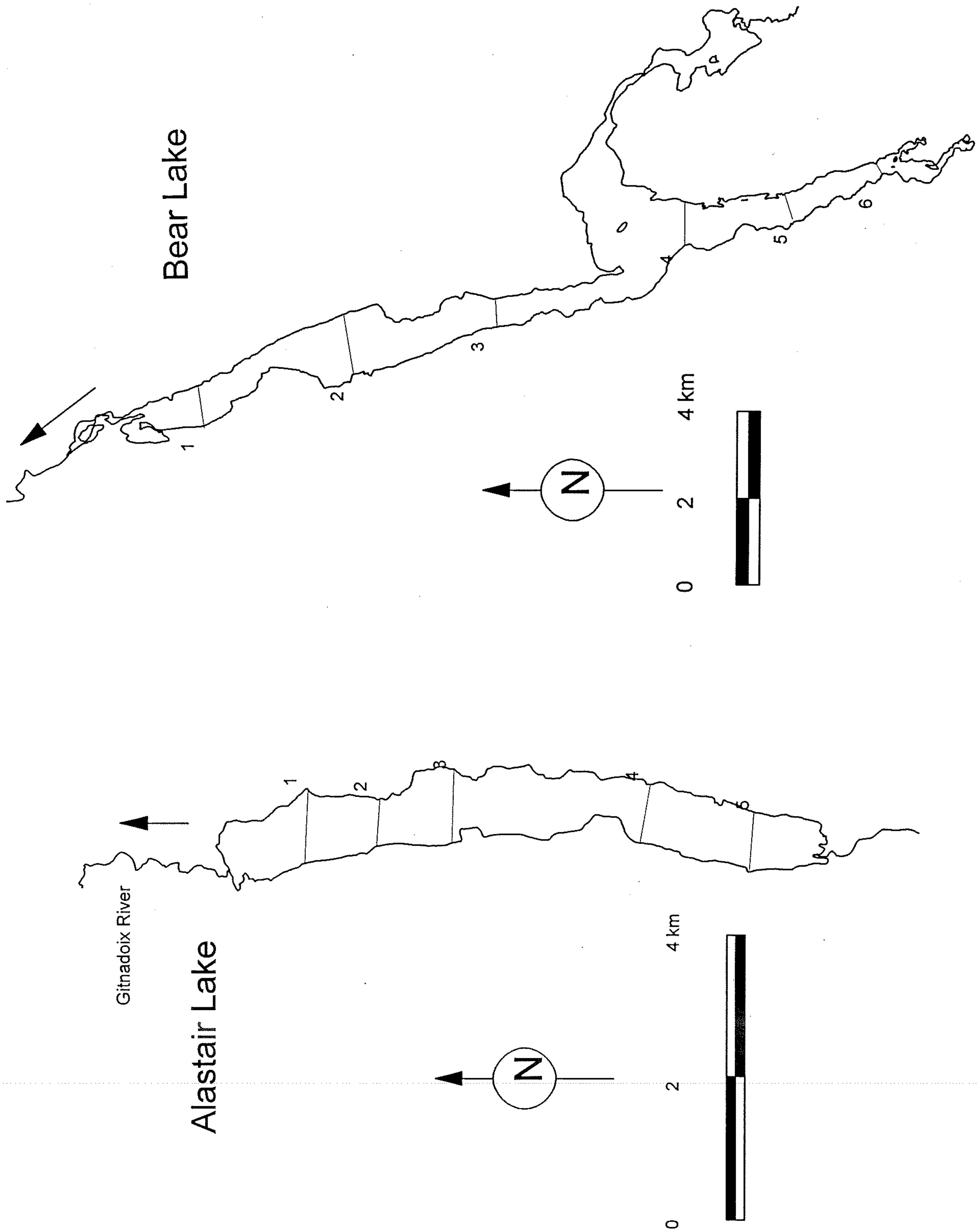


Fig. 1. Skeena River system and location of the study lakes.



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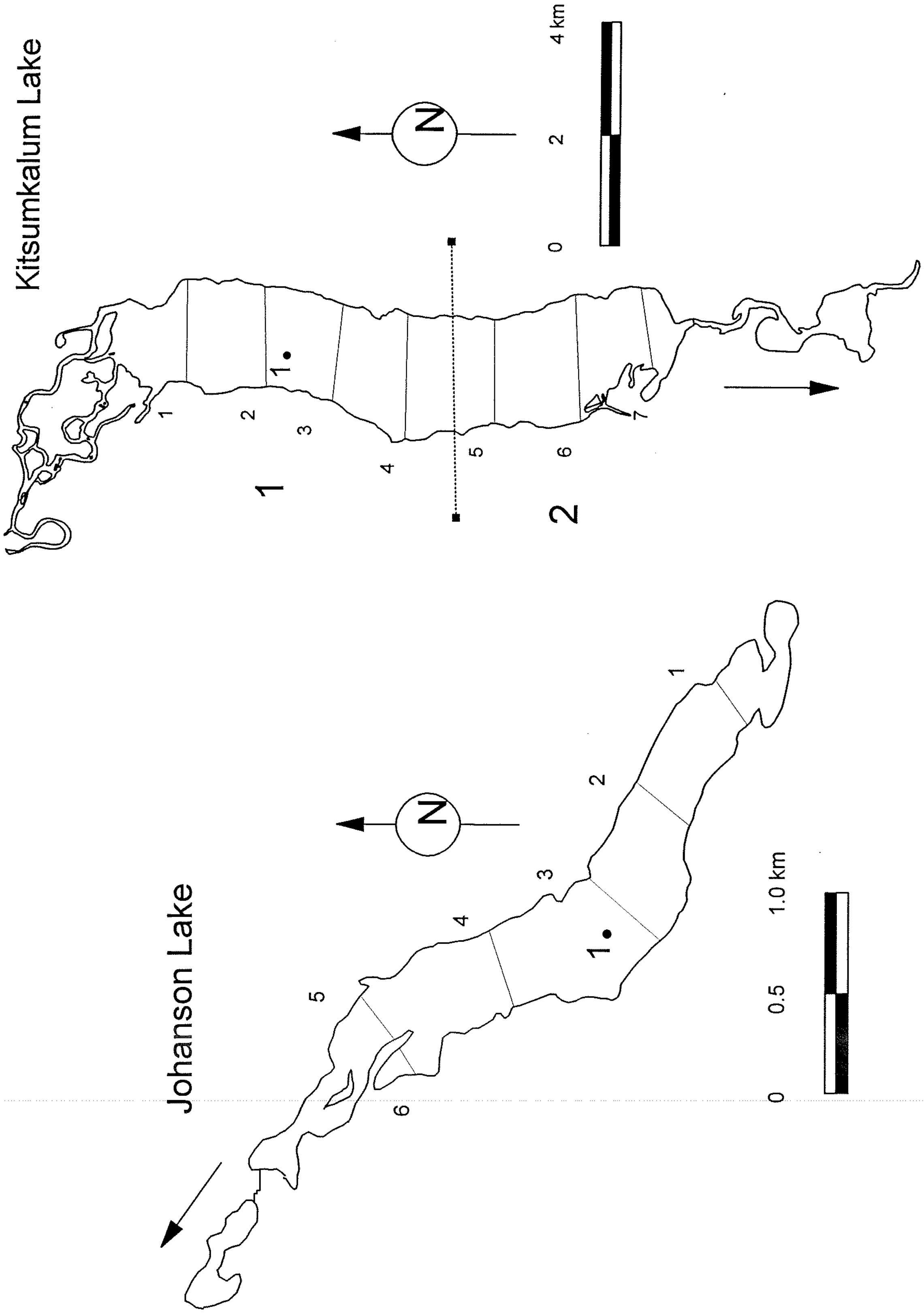

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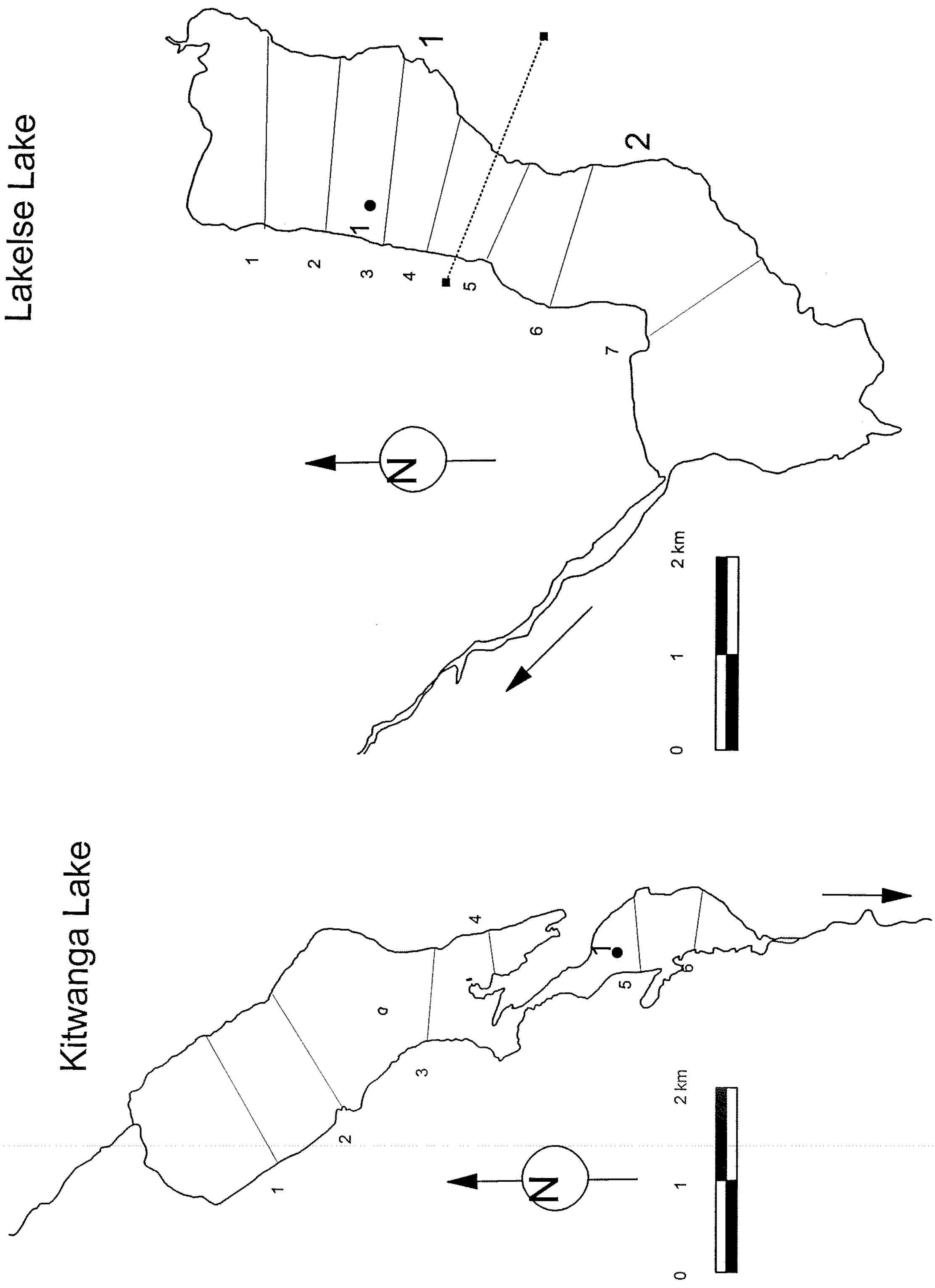

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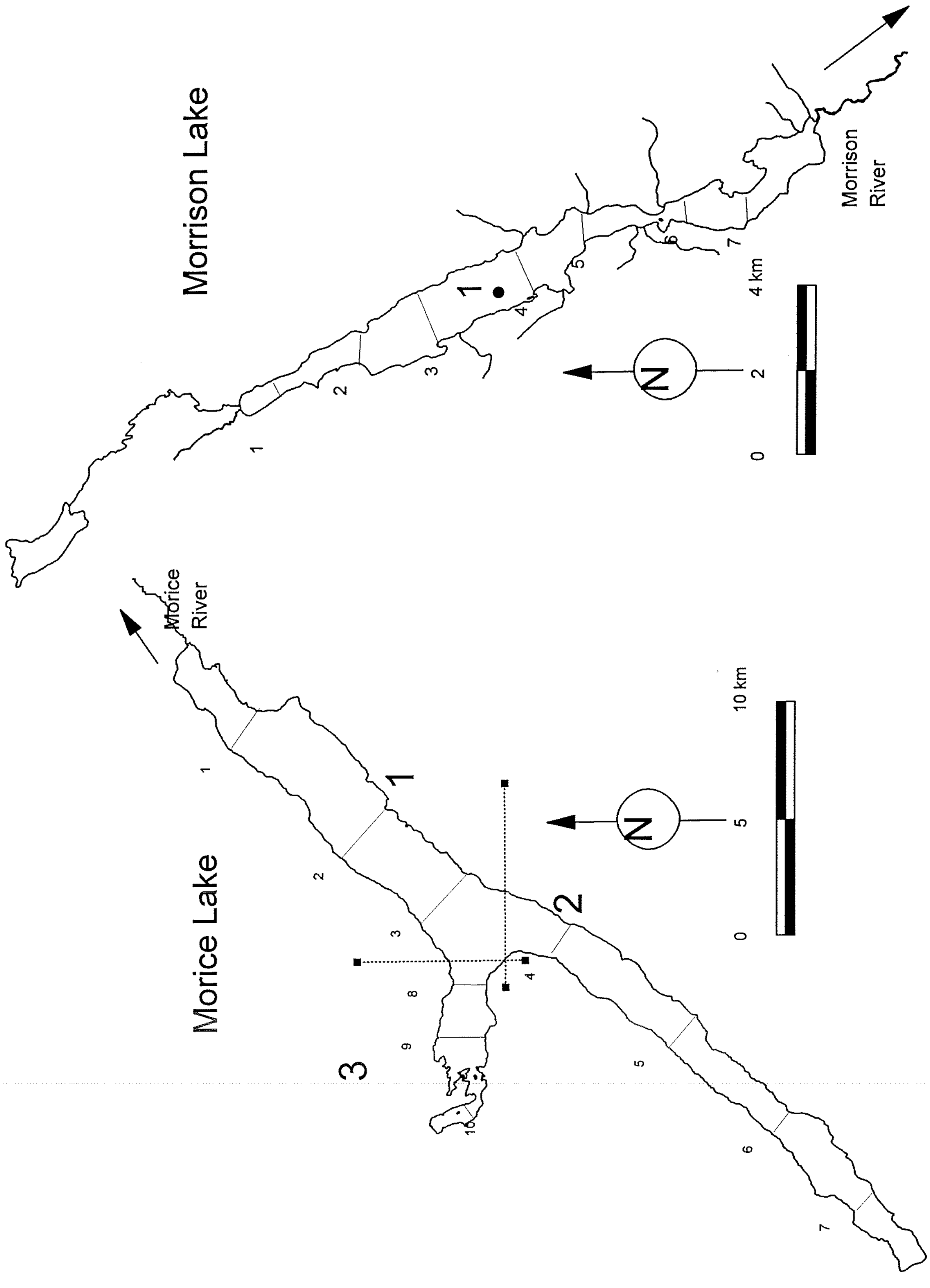

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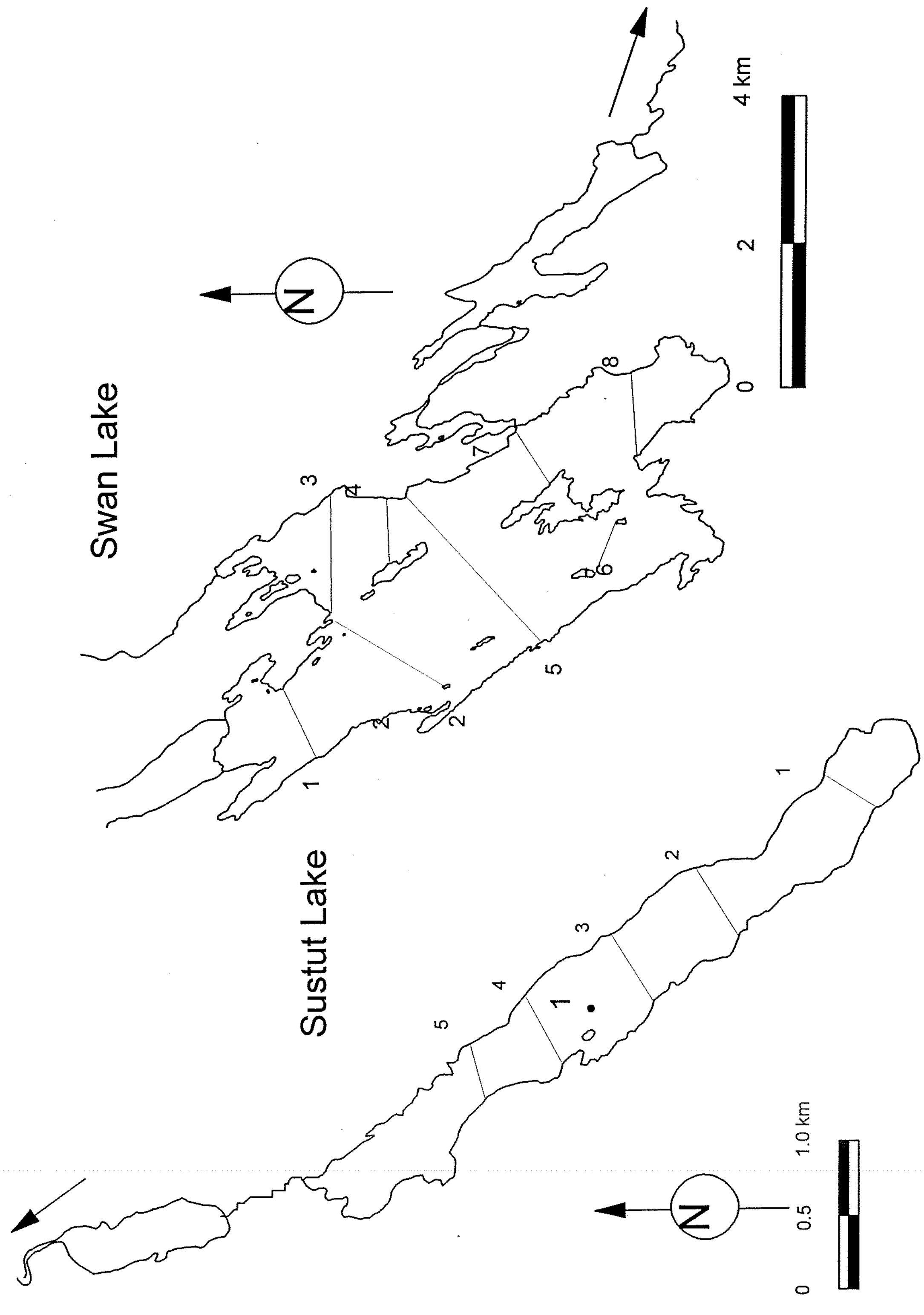

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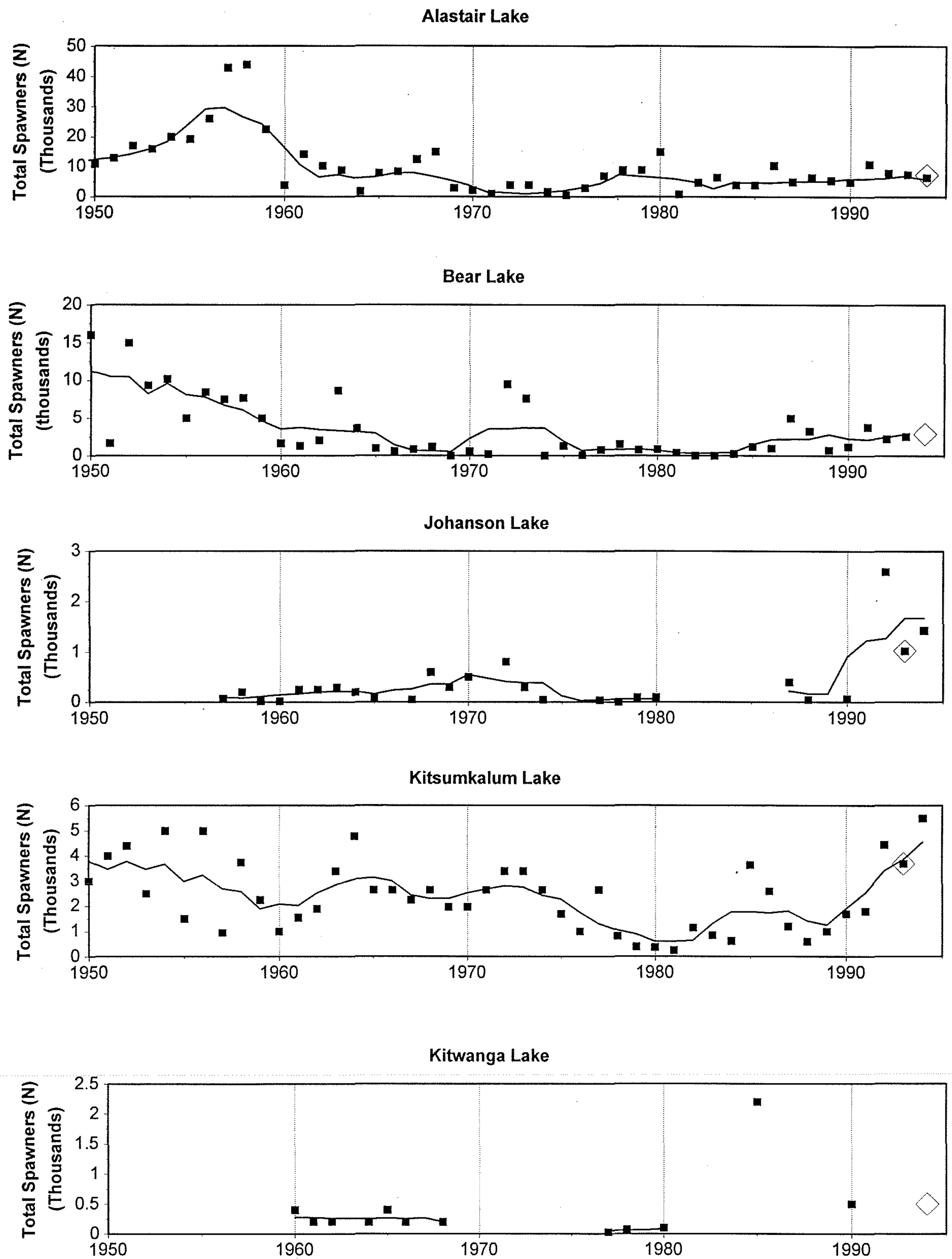


Fig. 7. Spawning escapements from 1950 to 1994 to Alastair, Bear, Johanson, Kitsumkalum, and Kitwanga lakes. The fry sampling year (diamond) and the running average of 5 points are shown (solid line). Data from L. Jantz (DFO, Prince Rupert).

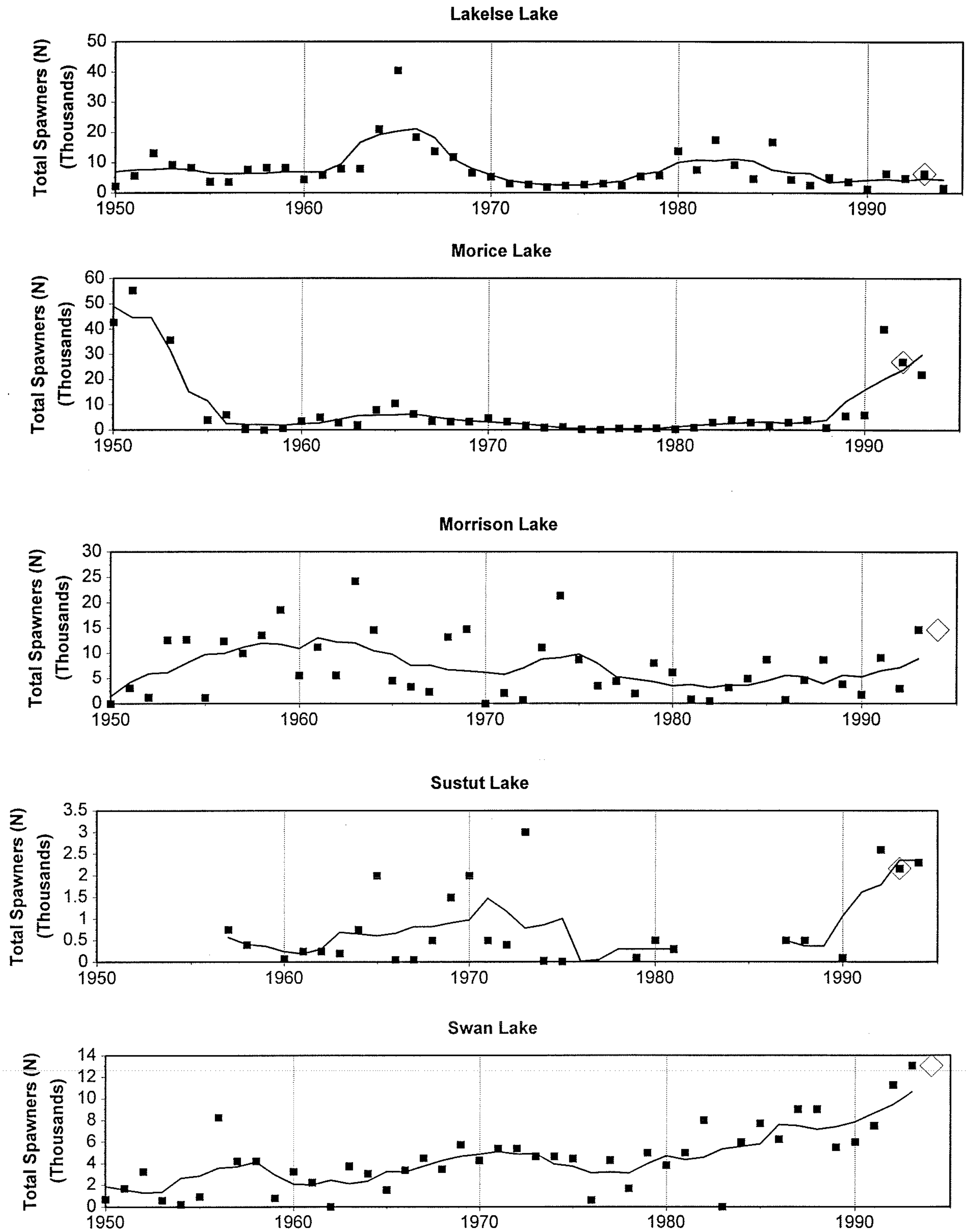
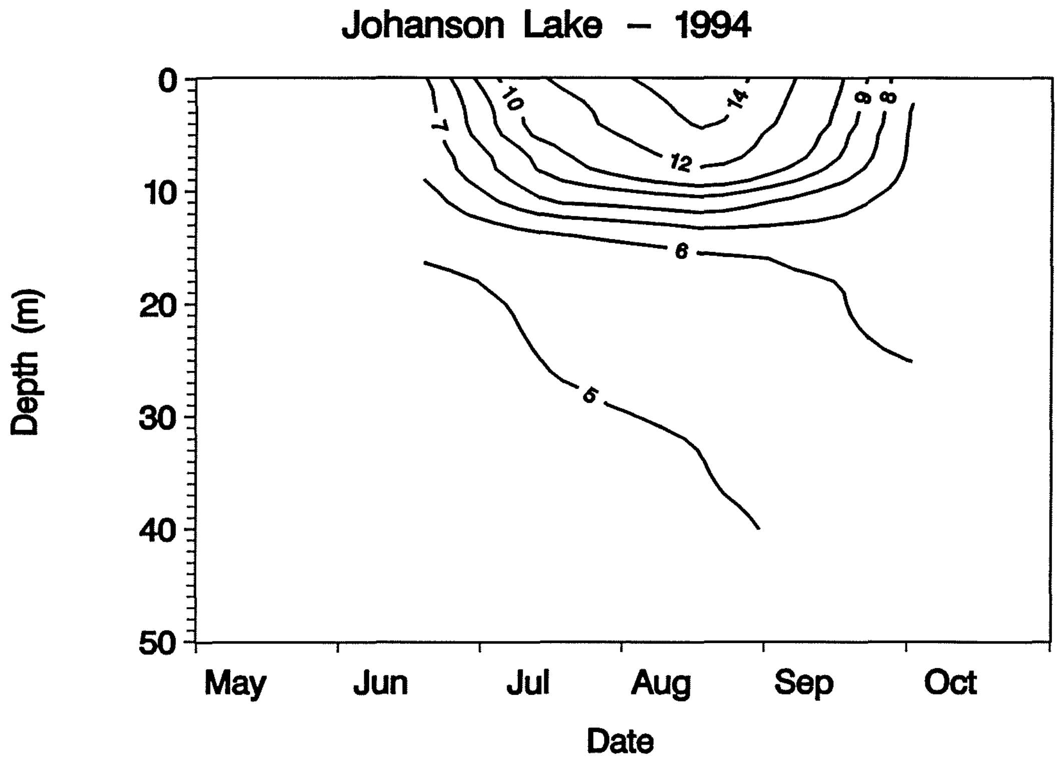
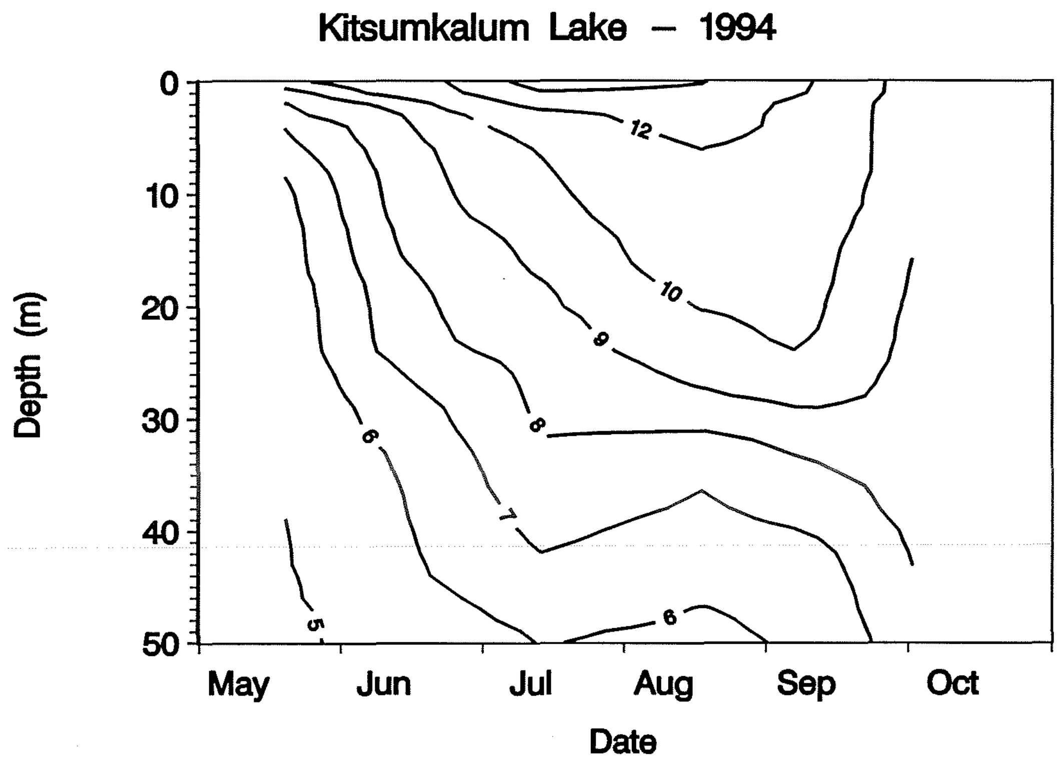


Fig. 8. Spawning escapements from 1950 to 1994 to Lakelse, Morice, Morrison, Sustut, and Swan lakes. The fry sampling year (diamond) and the running average of 5 points are shown (solid line). Data from L. Jantz (DFO, Prince Rupert).





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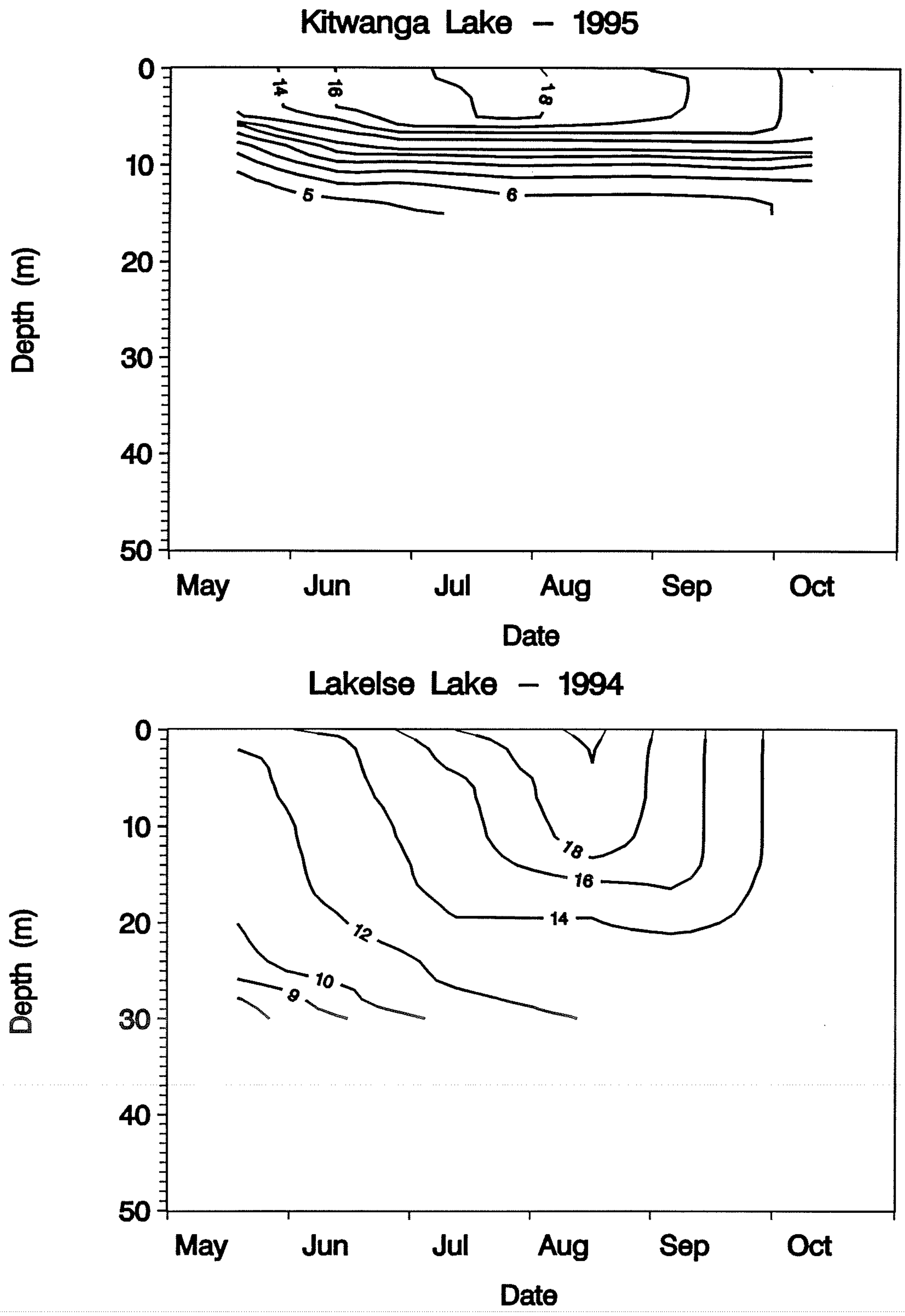

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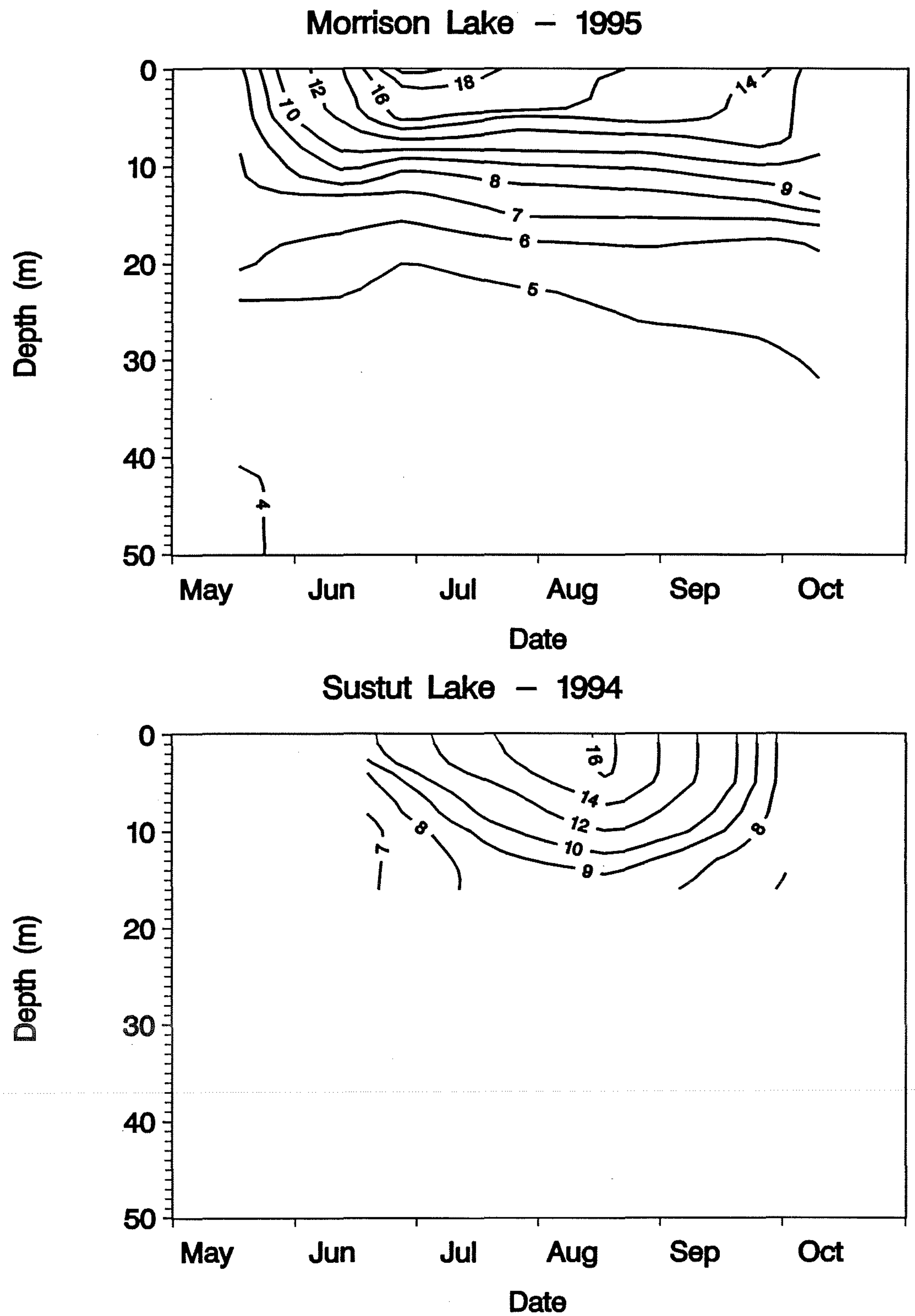

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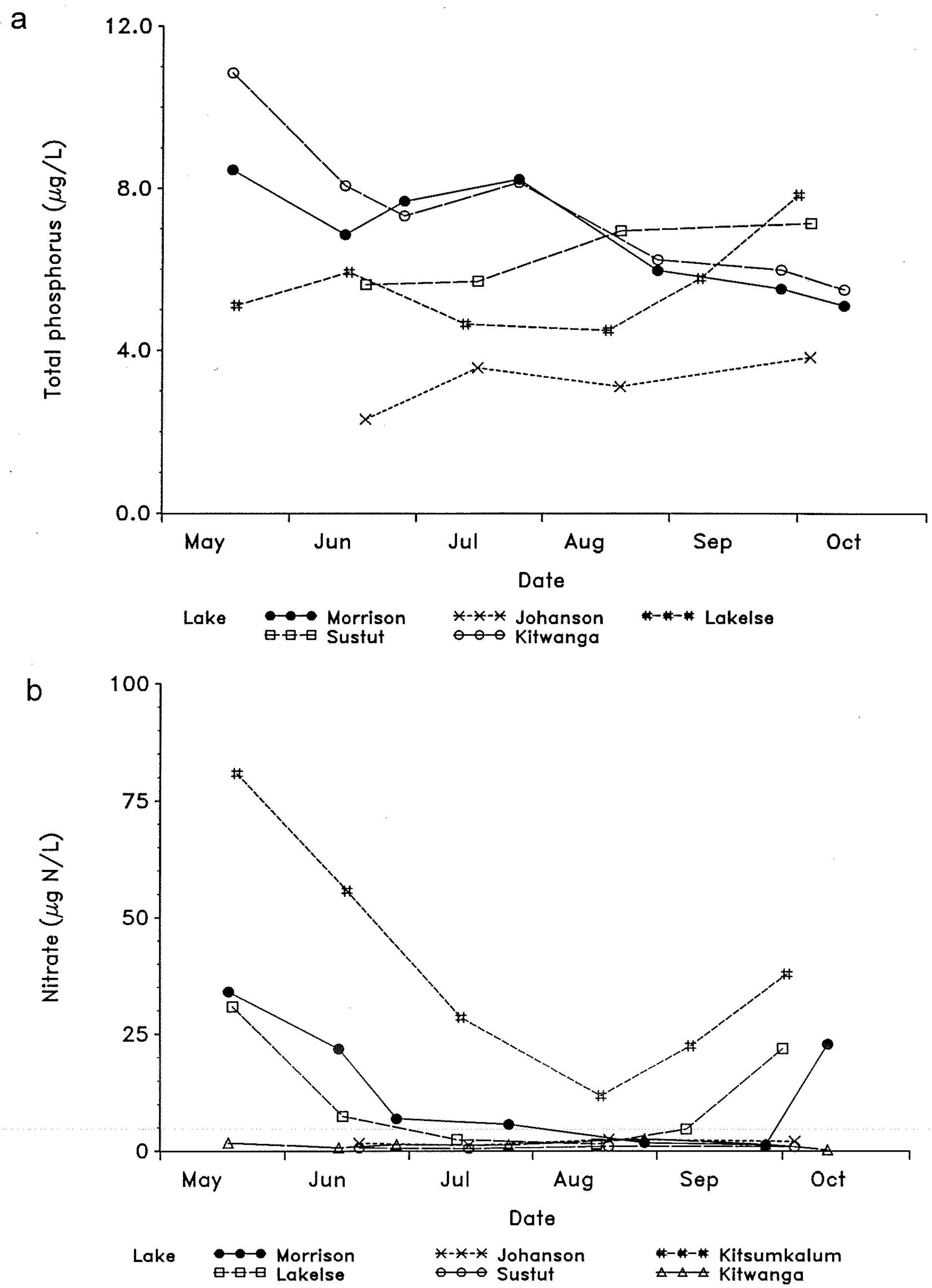

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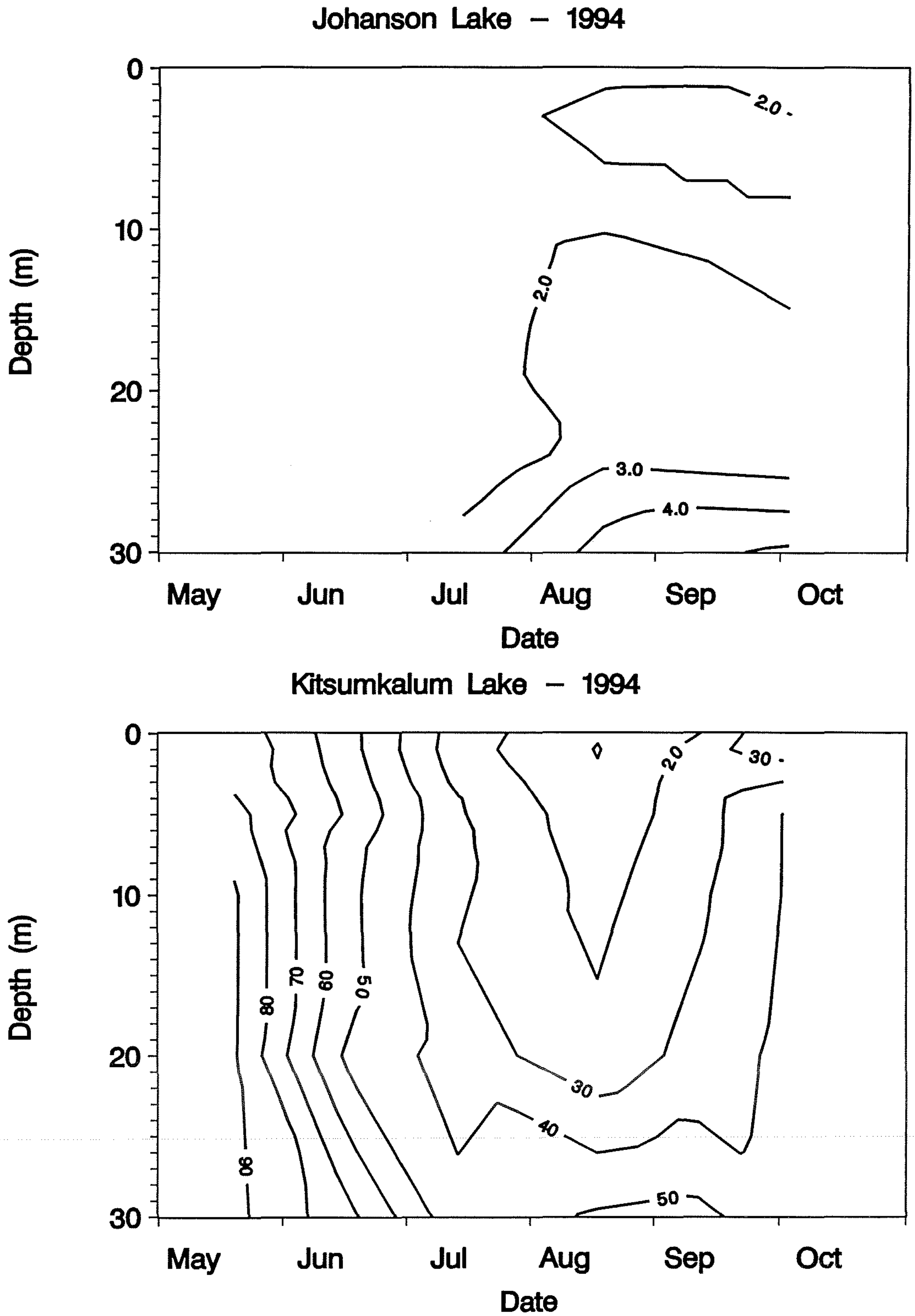

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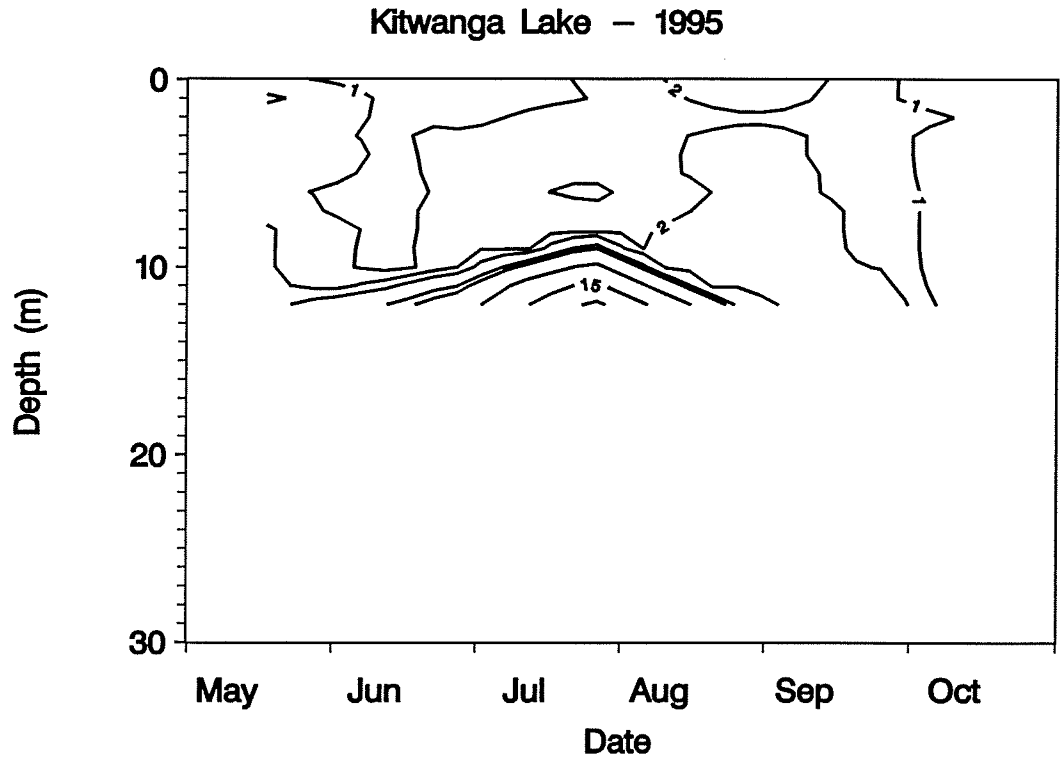

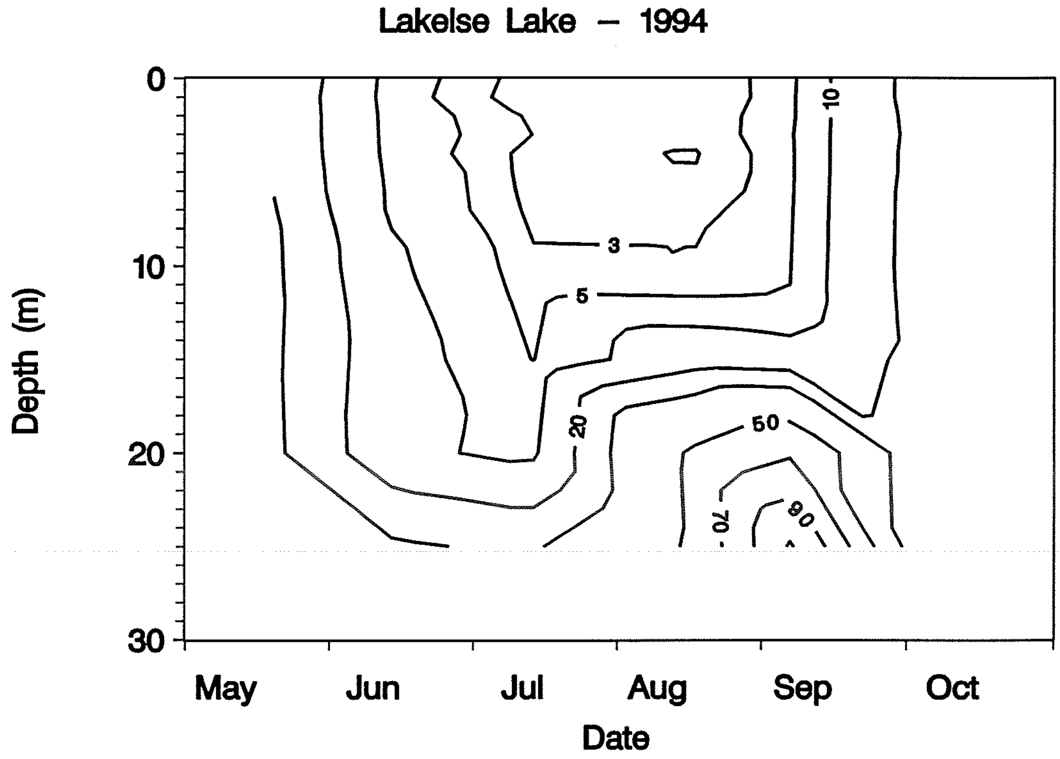

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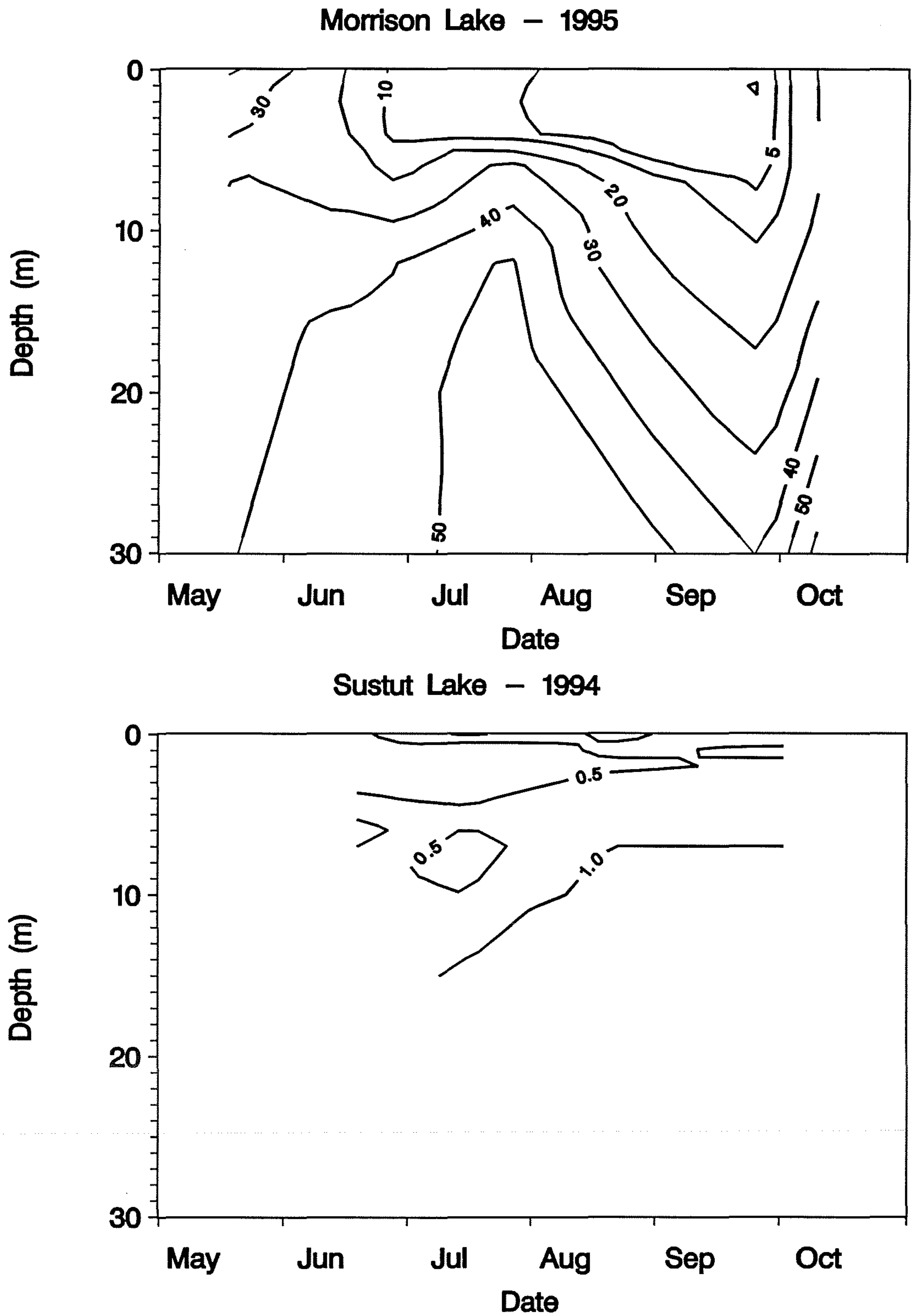

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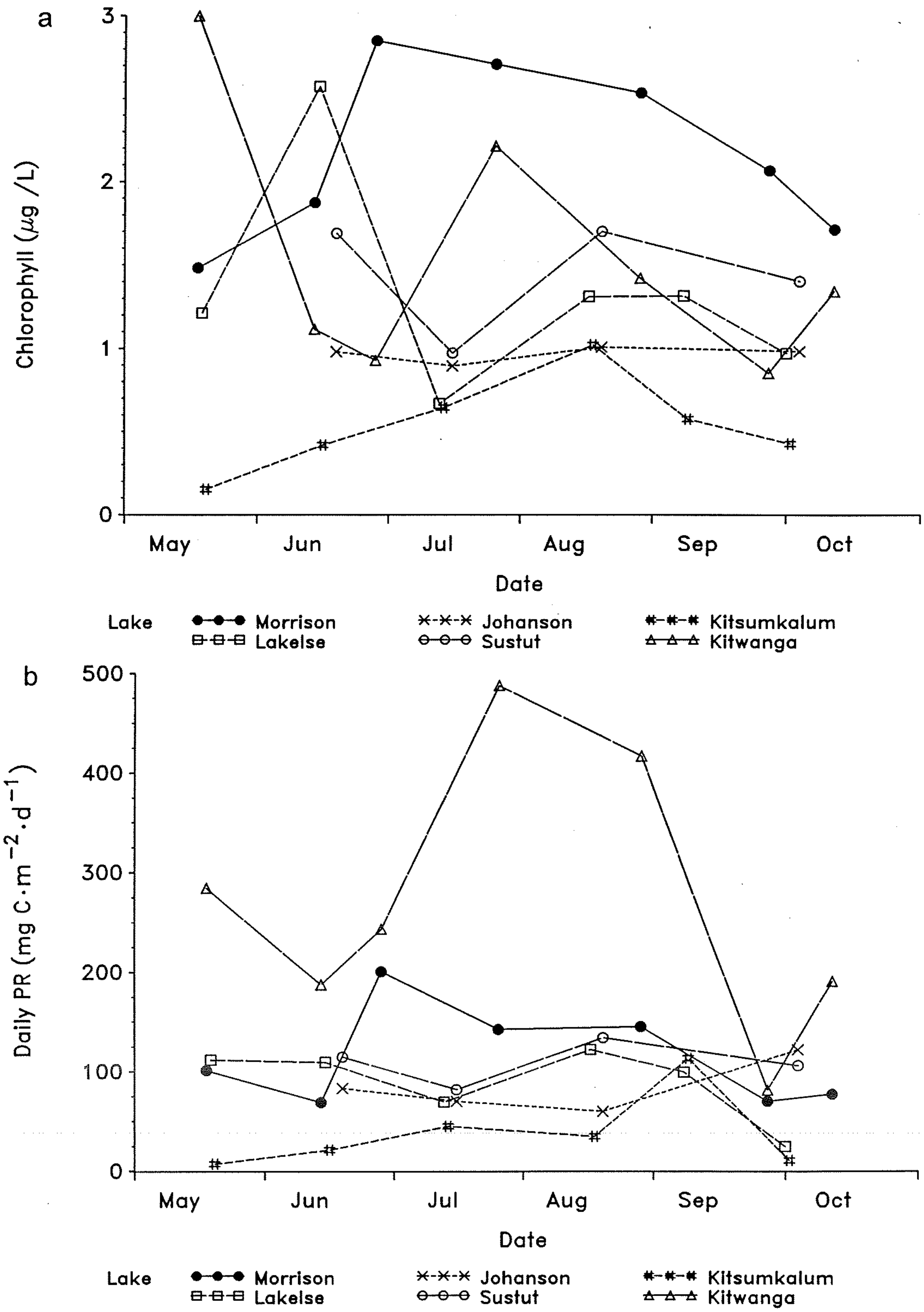

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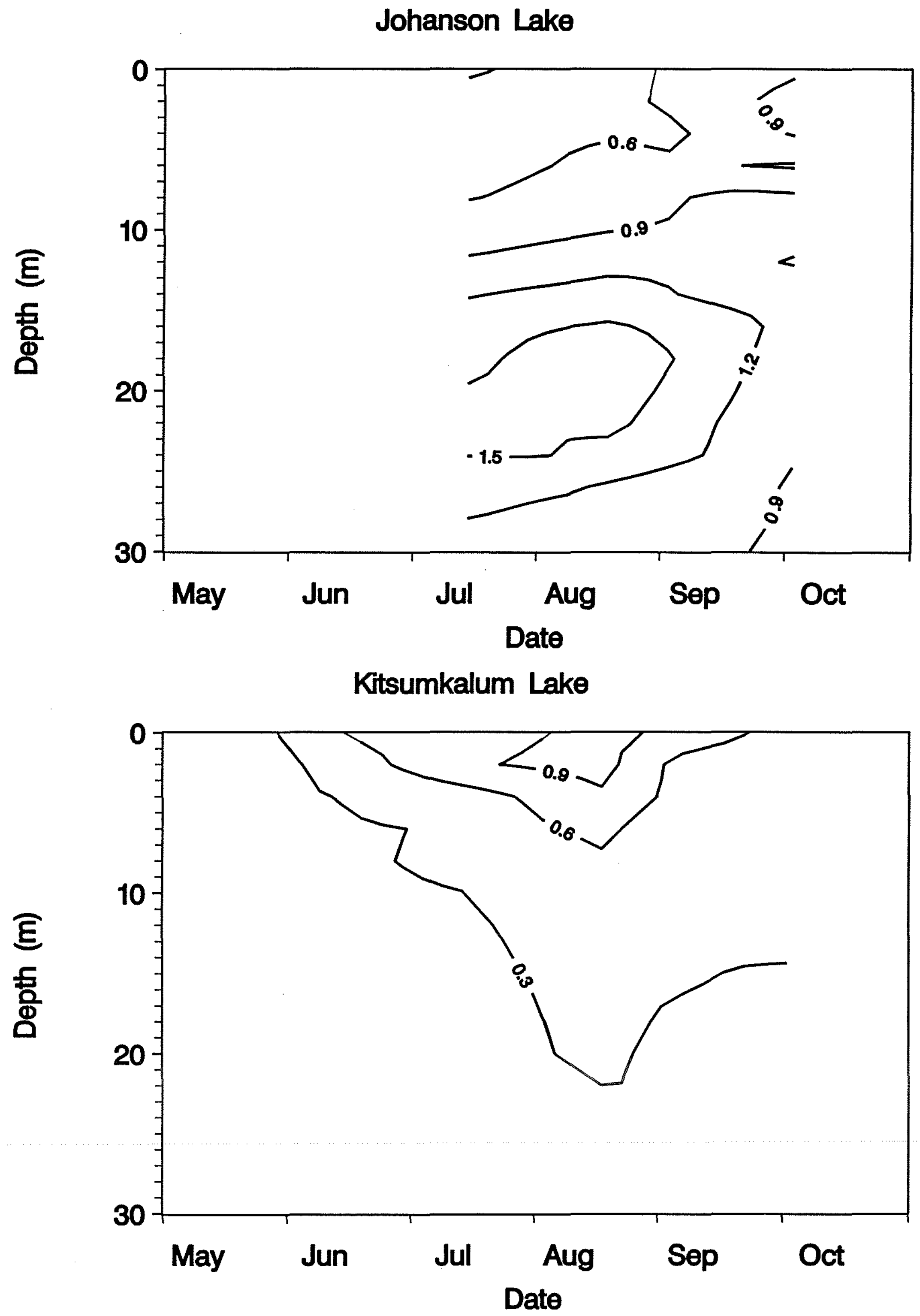

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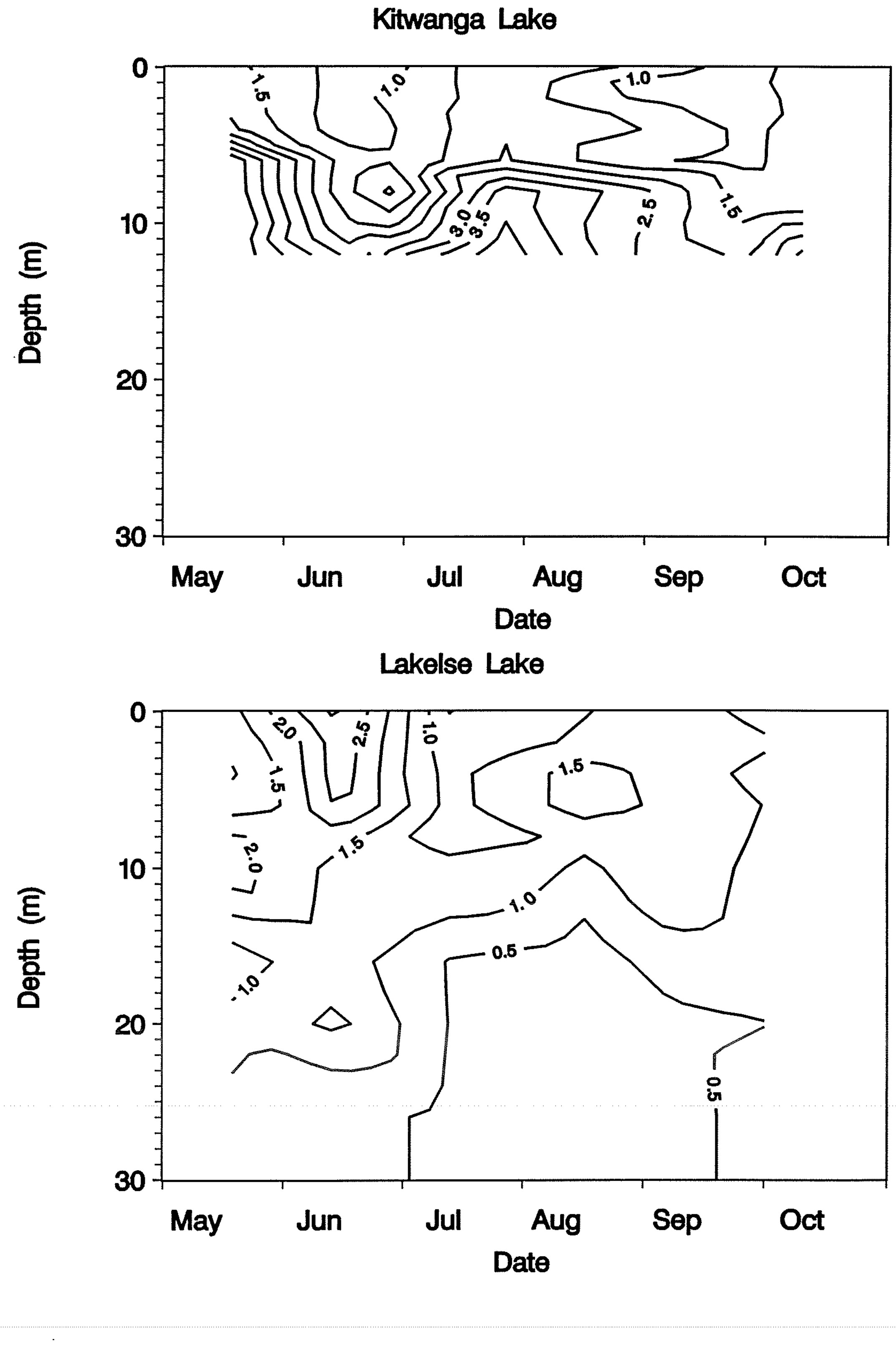

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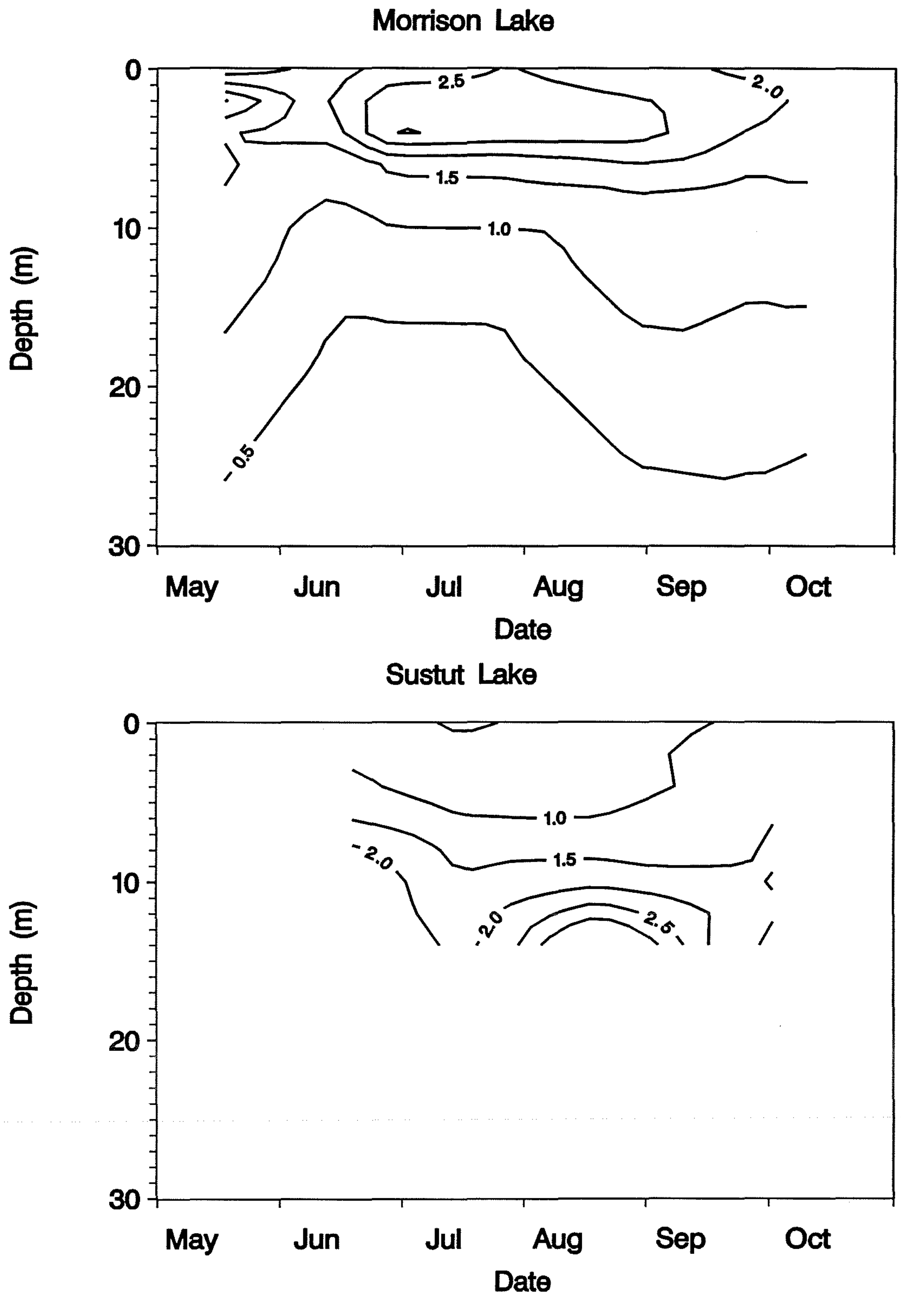

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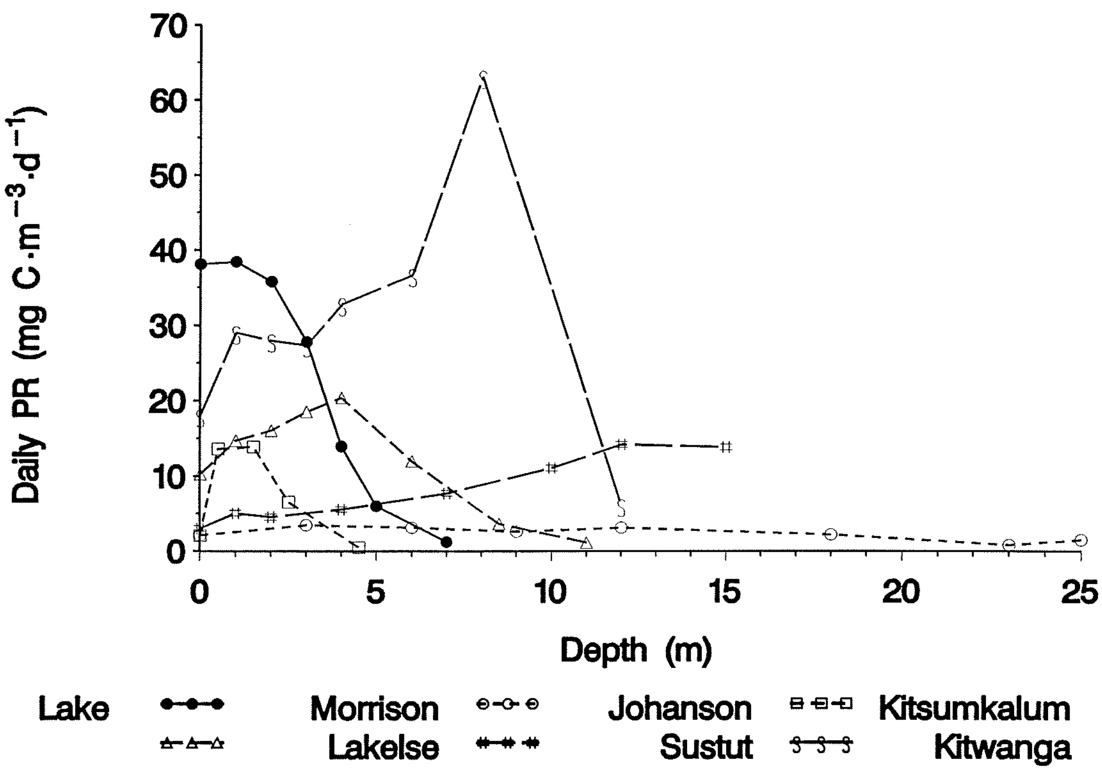

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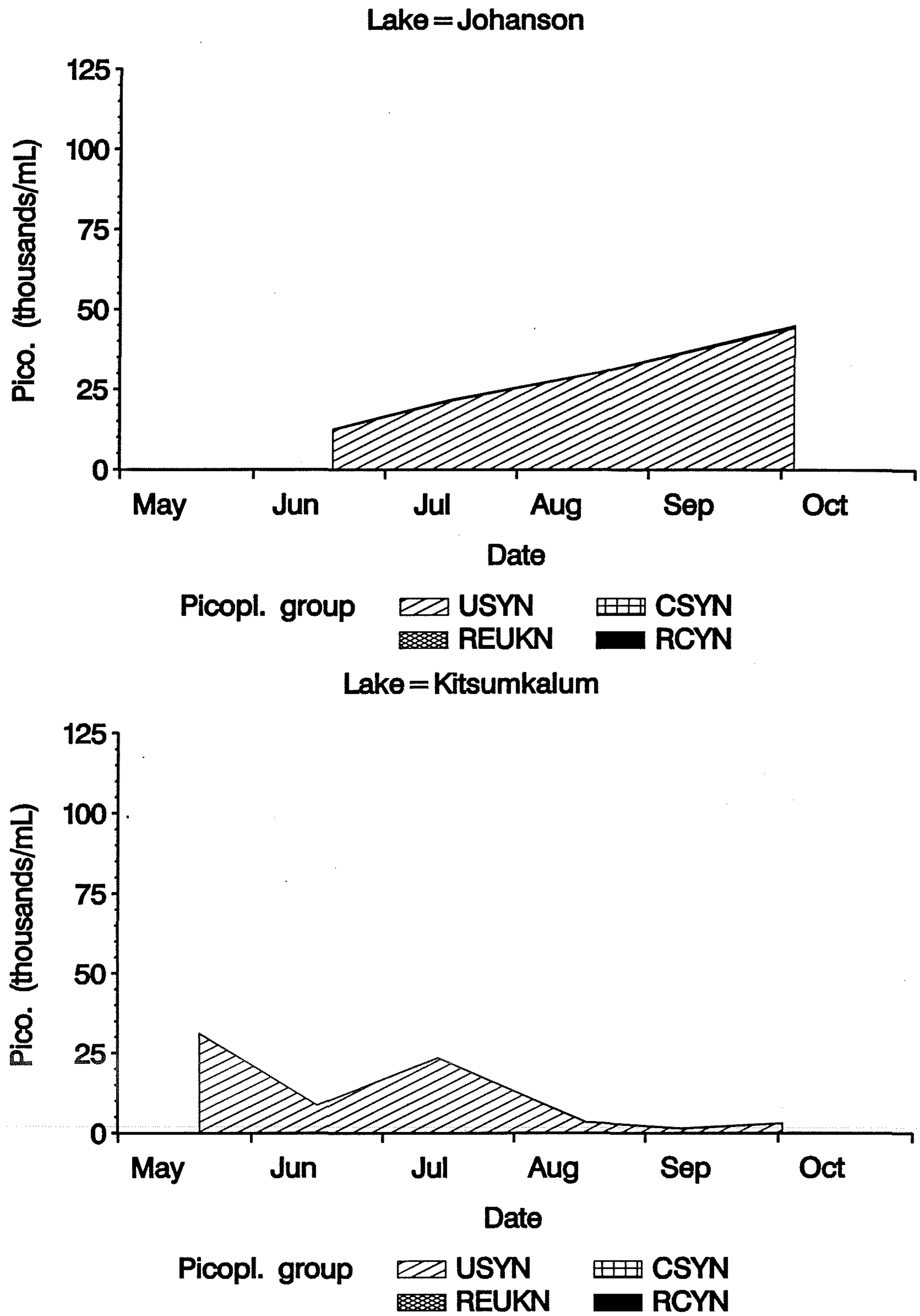

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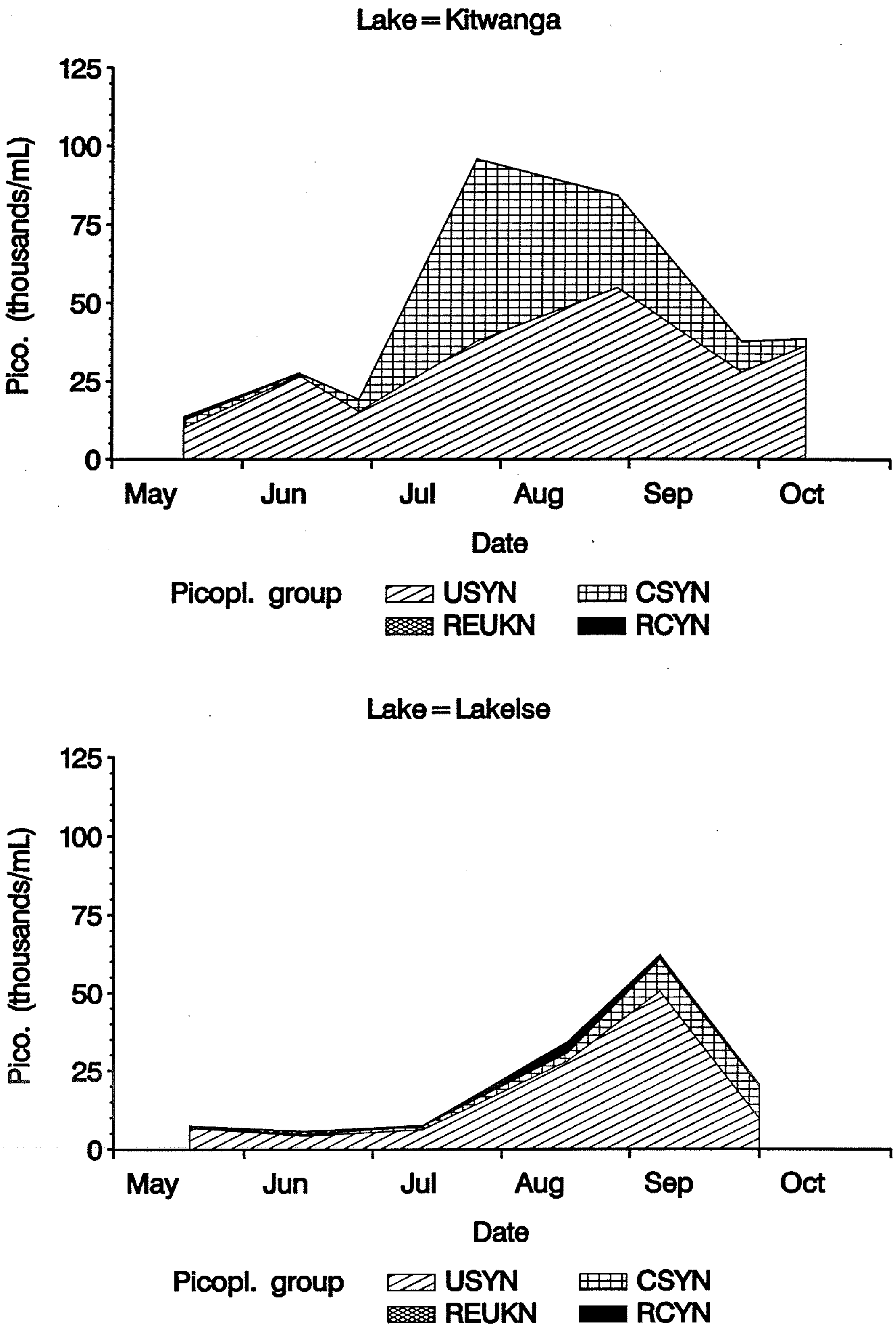

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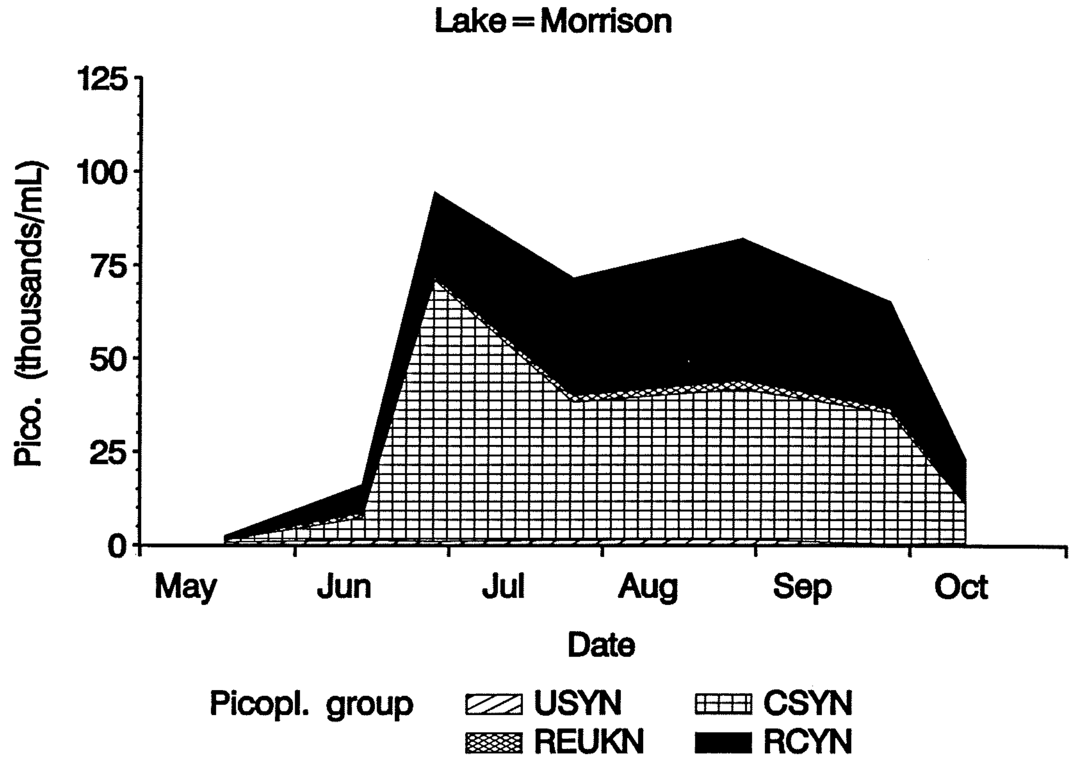


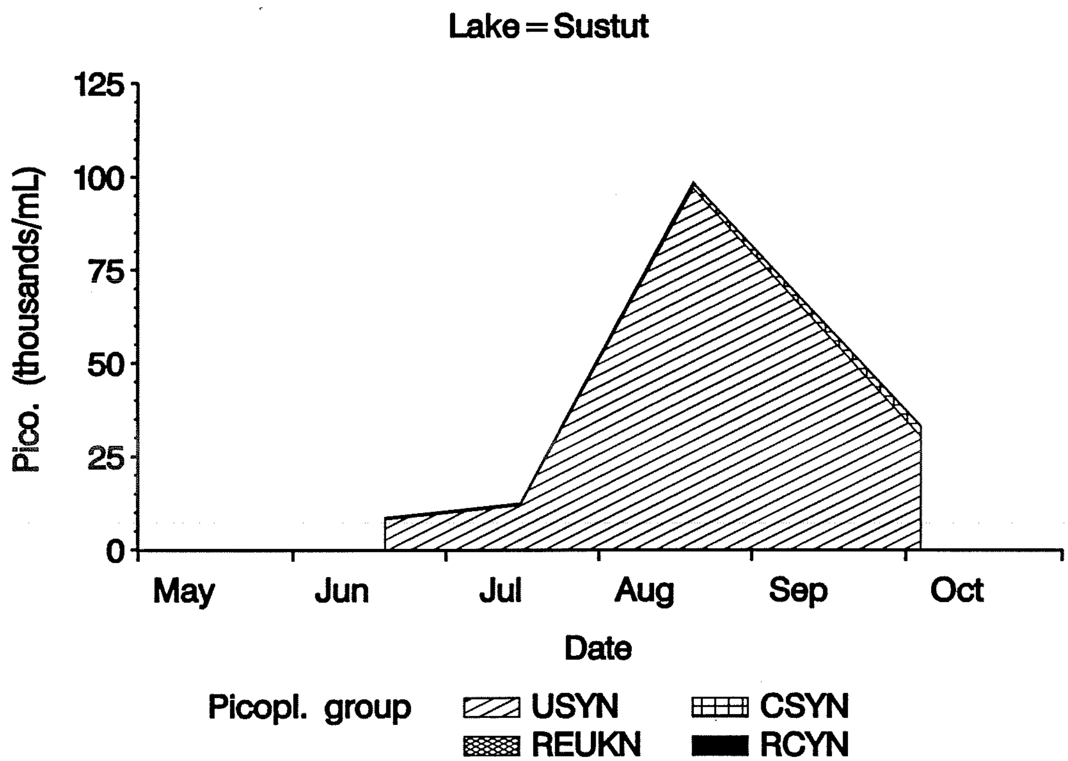
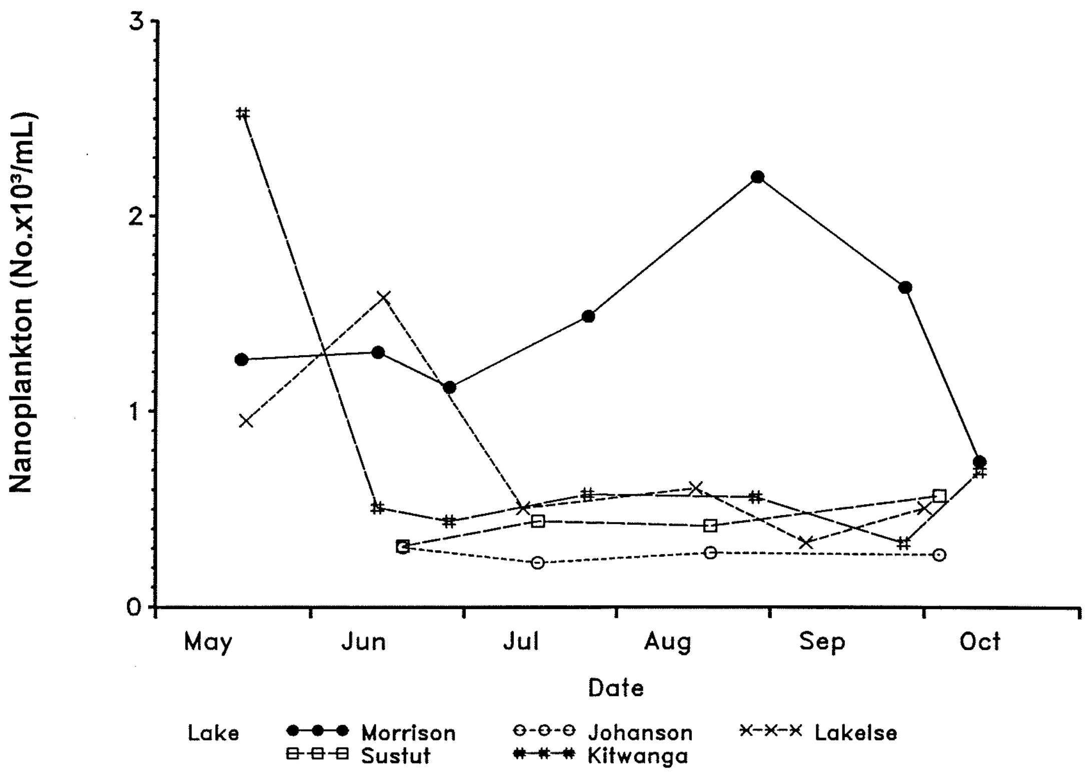


Fig. 23. Seasonal variation in picoplankton abundance and community structure in Morrison and Sustut lakes.



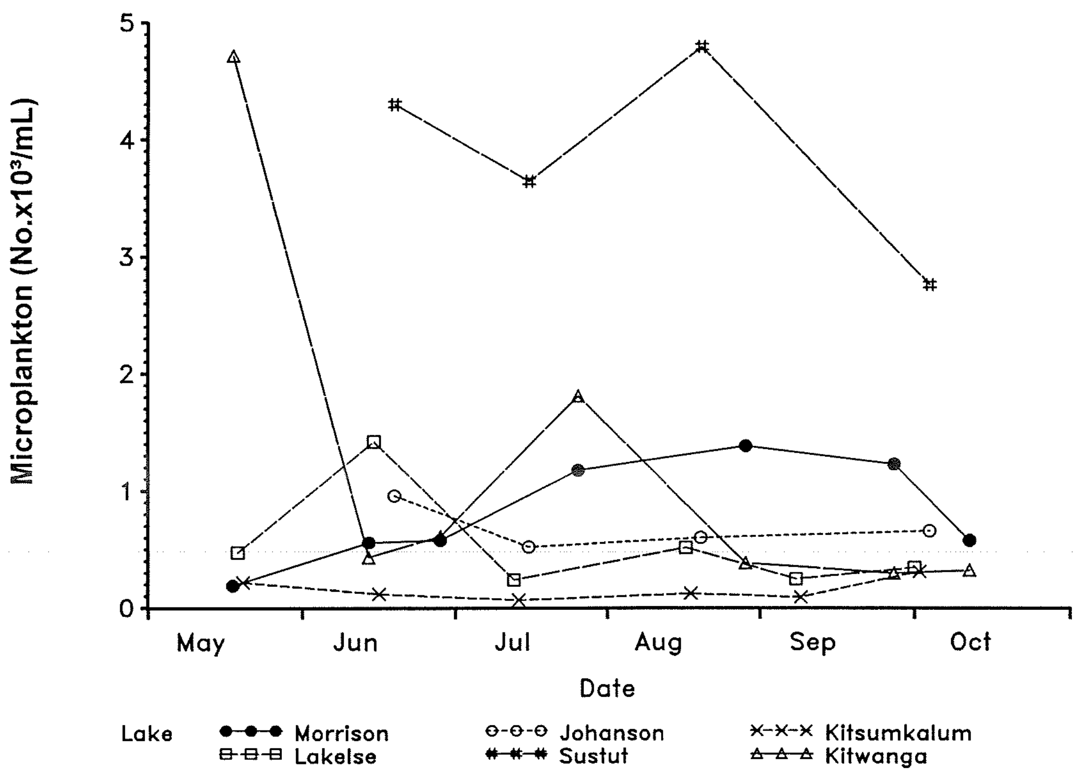
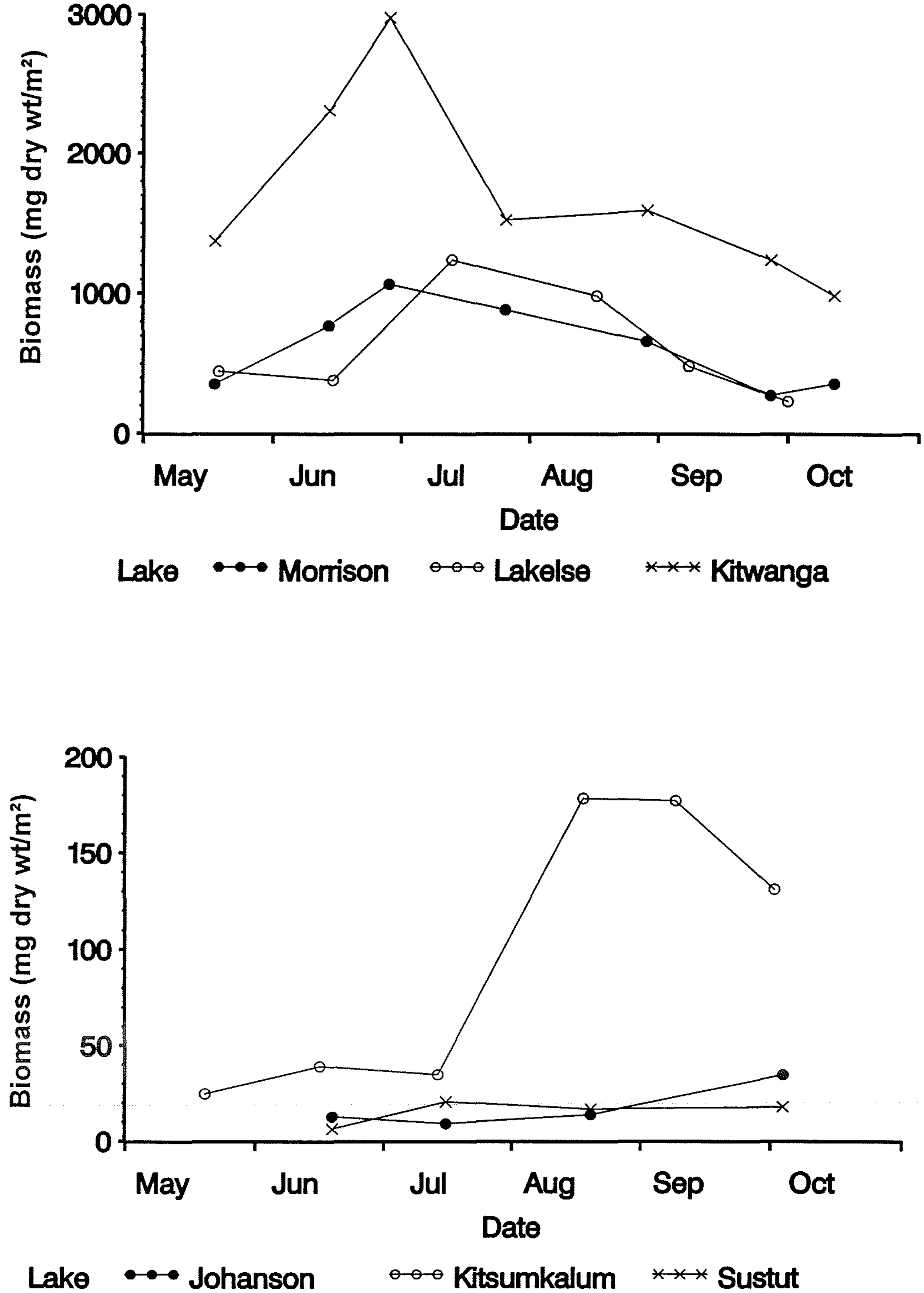


Fig. 24. Seasonal variation in nanoplankton (2-20 μm) and microplankton (>20 μm) numbers inthe study lakes.



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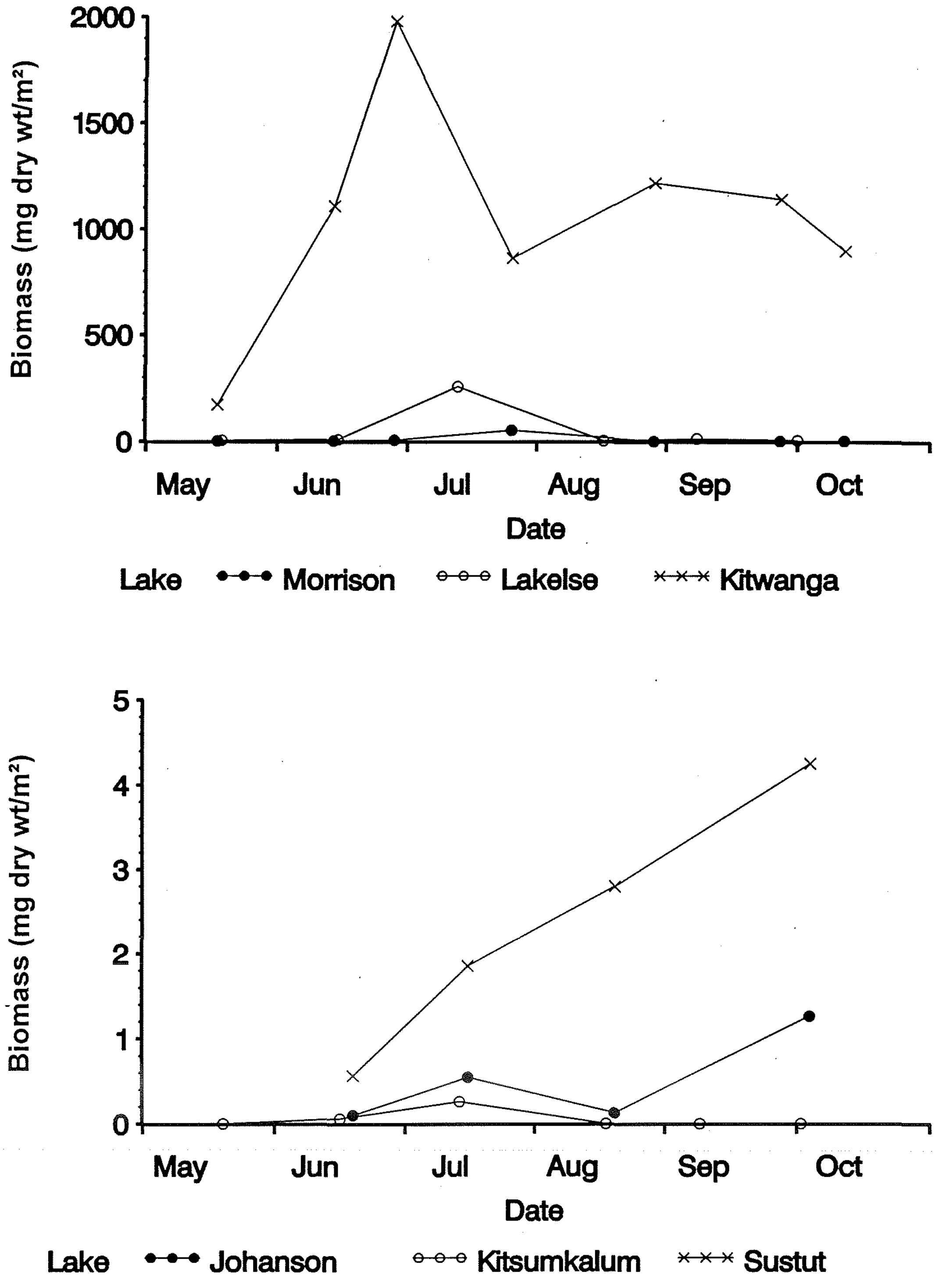
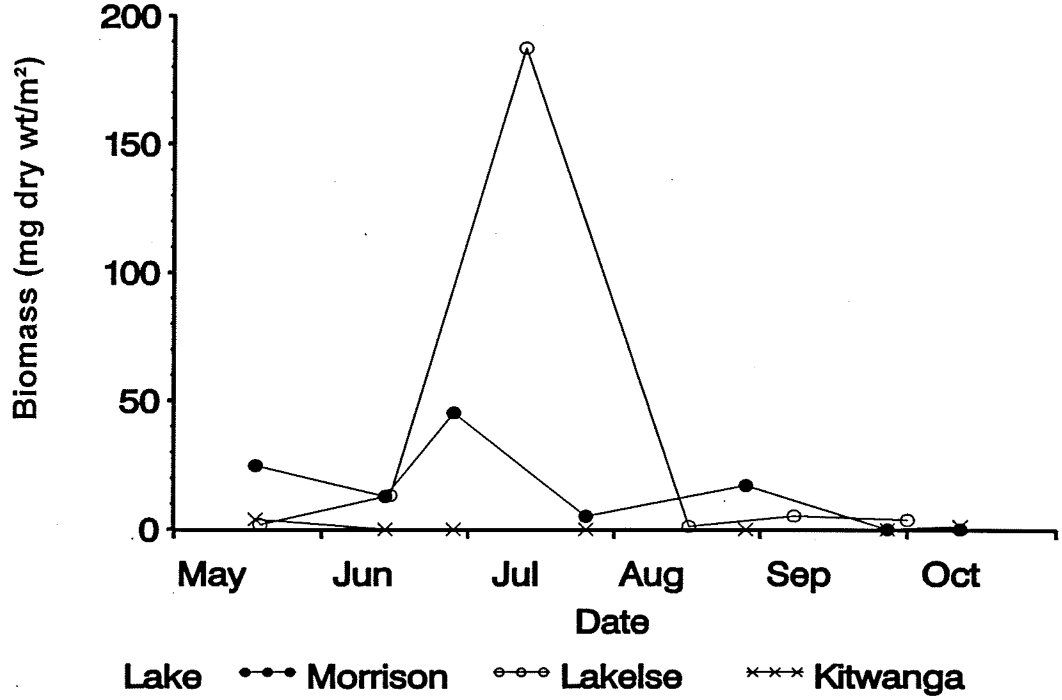


Fig. 26. Seasonal variation in *Daphnia* biomass in the study lakes. Note the different scales on the figures.



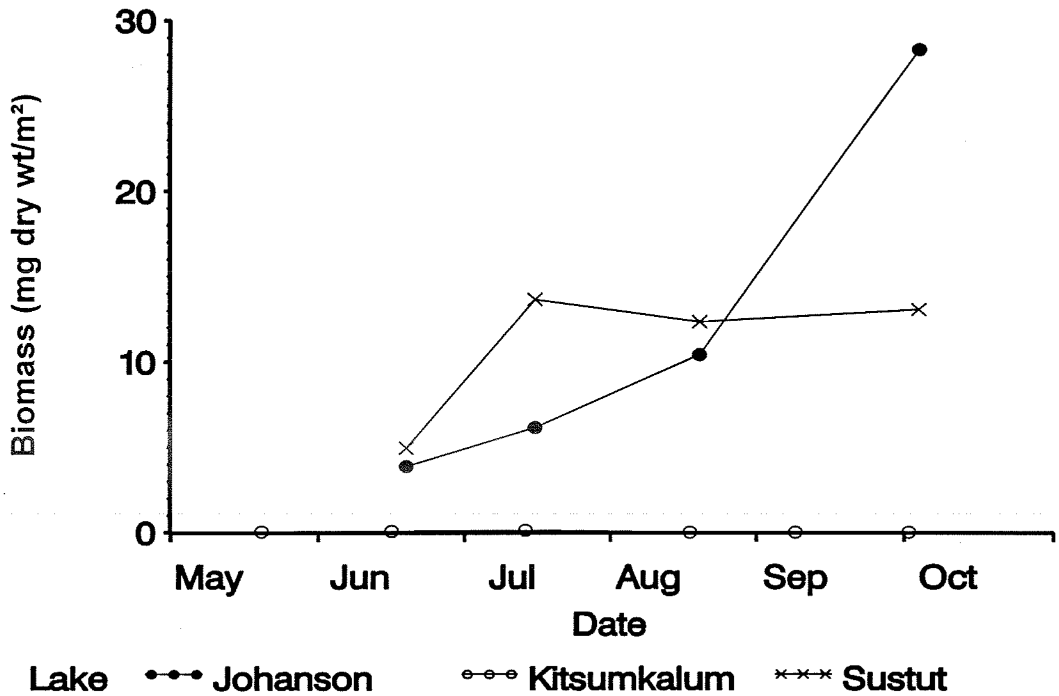


Fig. 27. Seasonal variation in biomass of Bosminidae. Note the different scales on the figures.

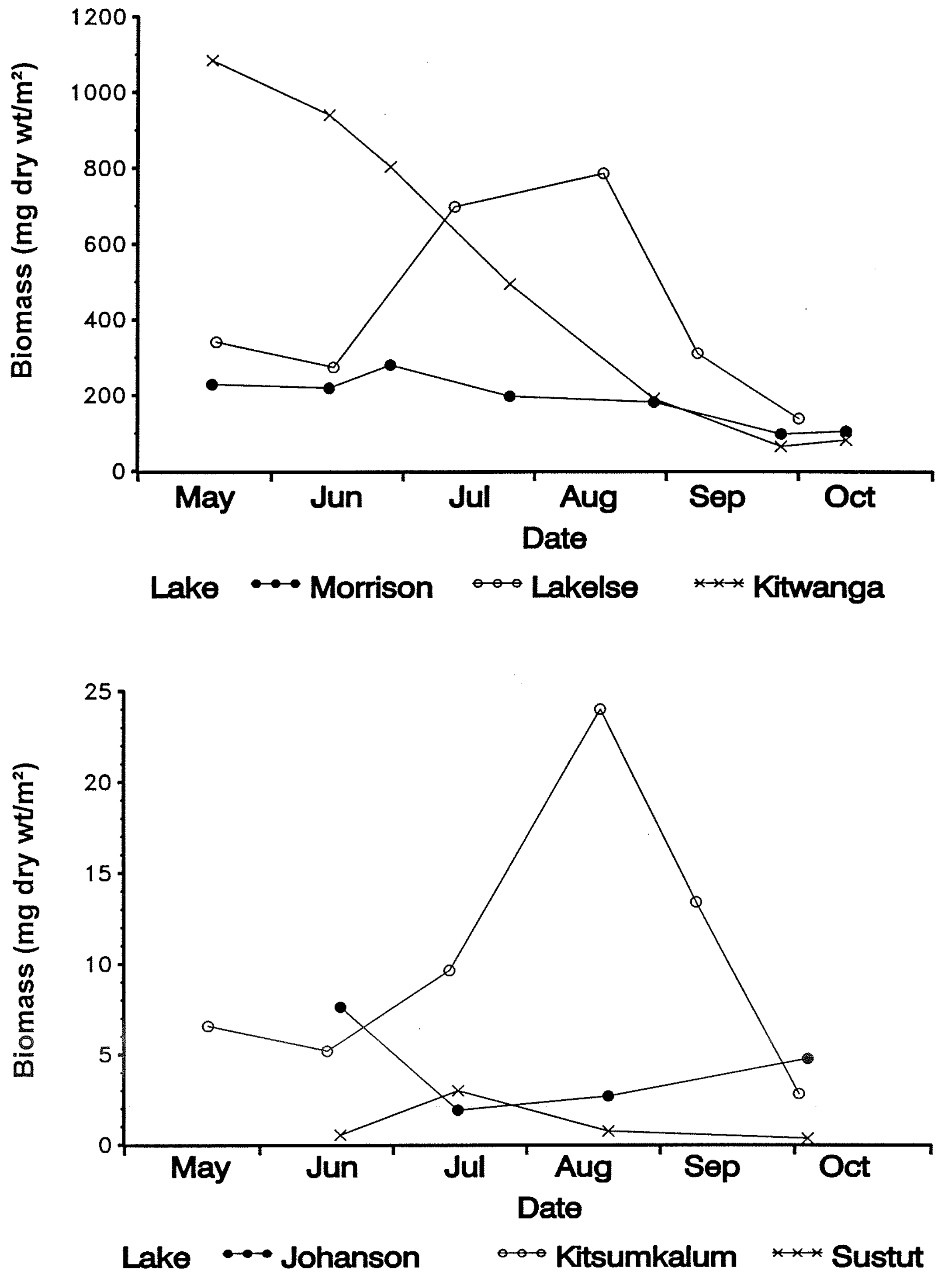
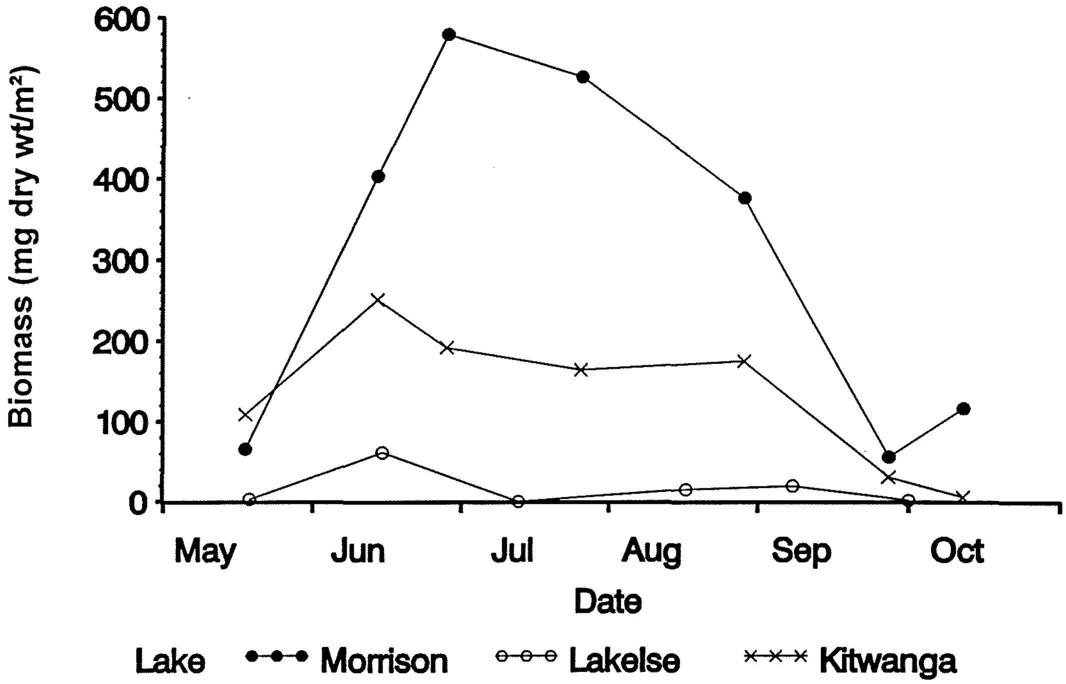


Fig. 28. Seasonal variation in biomass of Cylopidae. Note the different scales on the figures.



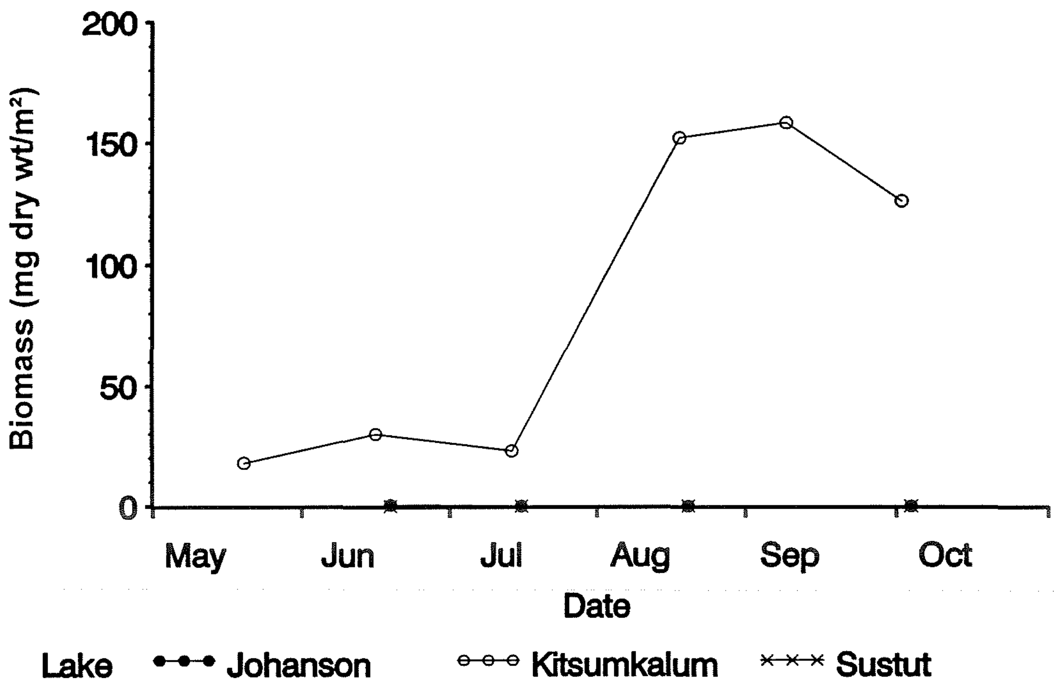


Fig. 29. Seasonal variation in biomass of Diaptomidae. Note the different scales on the figures.

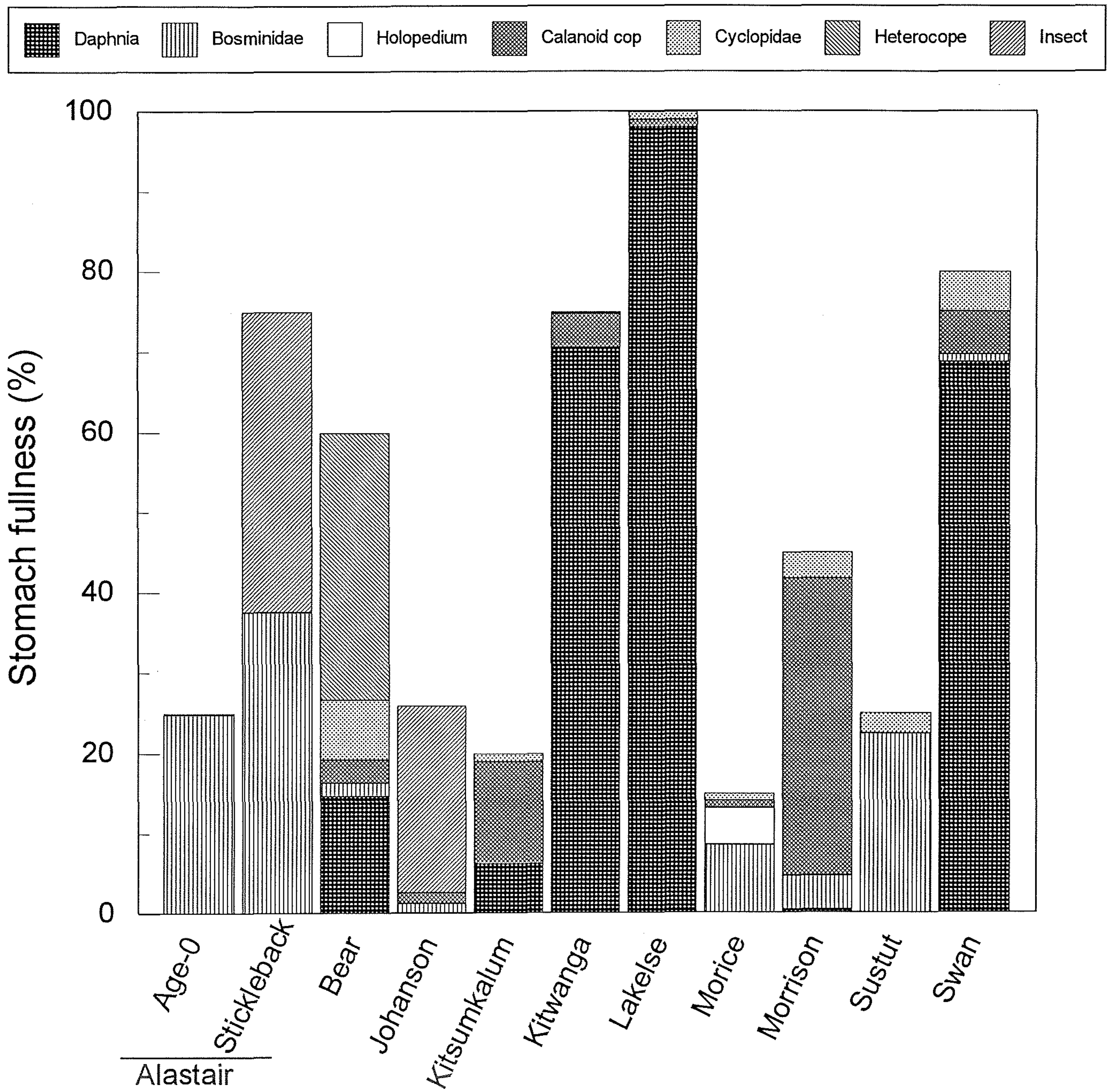


Fig. 30. Stomach fullness and composition of stomach contents from the study lakes. All data are for age-0 sockeye except for bar labelled stickleback. Calanoid copepod category is made up of *Leptodiaptomus* and *Epischura*. Insects are primarily chironomids.

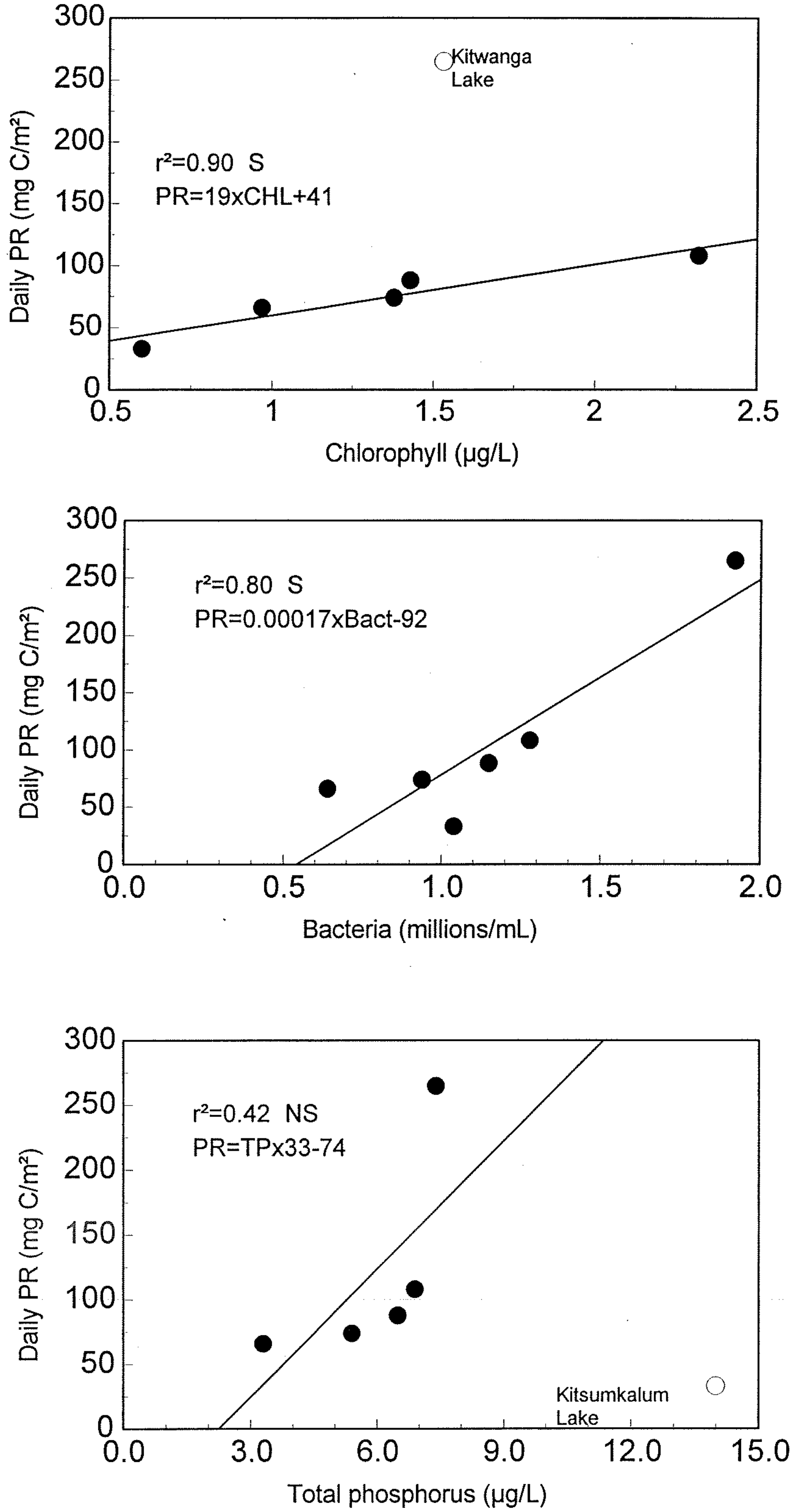


Fig. 31. Relationship between seasonal averages of daily PR and three commonly used indicators of trophic status.

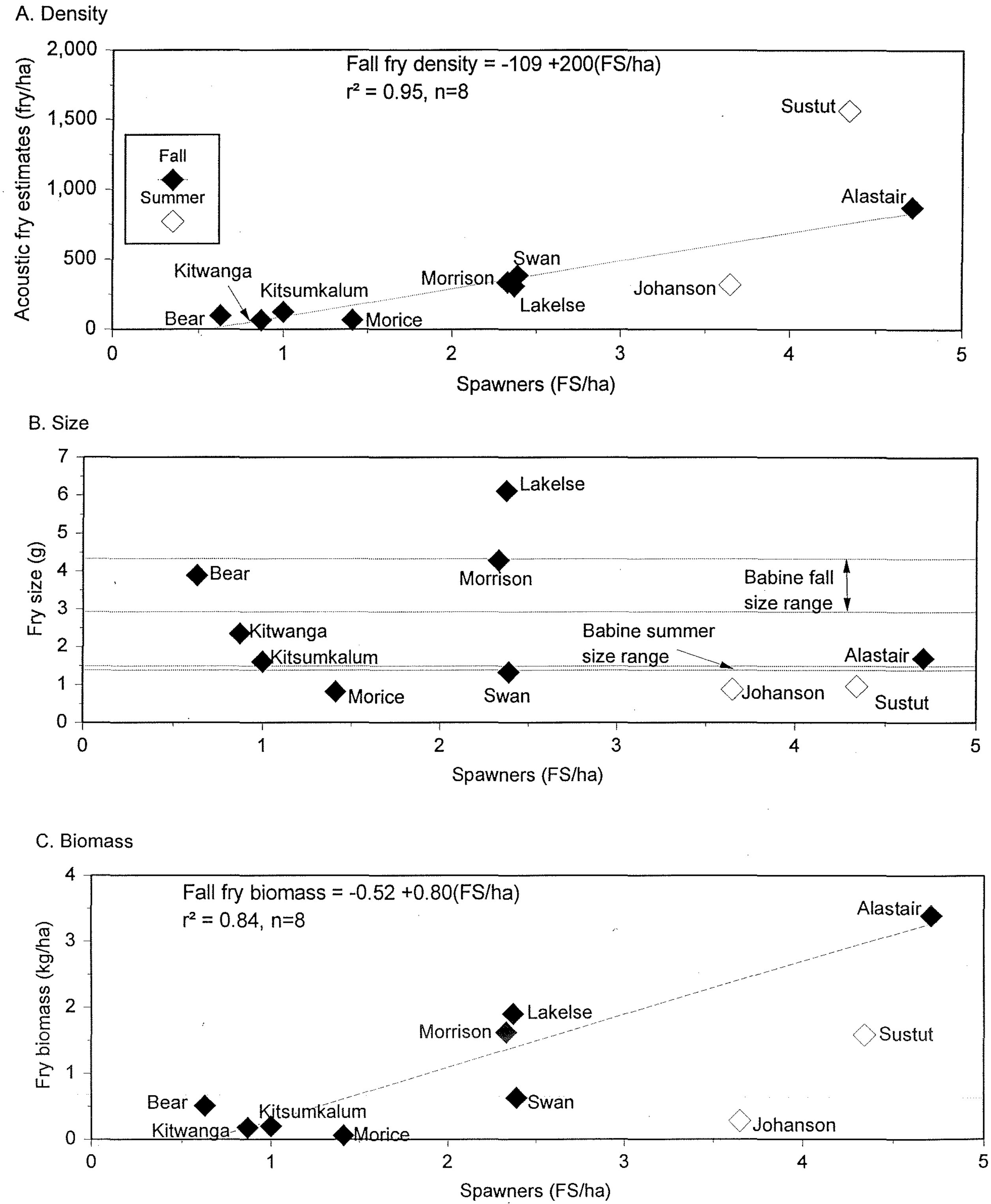


Fig 32. Density, size and biomass of fry in the study lakes of the Skeena River. The size range found in Babine lake during summer and fall surveys is shown (dotted lines) for comparison purposes. Johanson and Sustut lakes were surveyed in late August rather than in October and are not included in the regressions.